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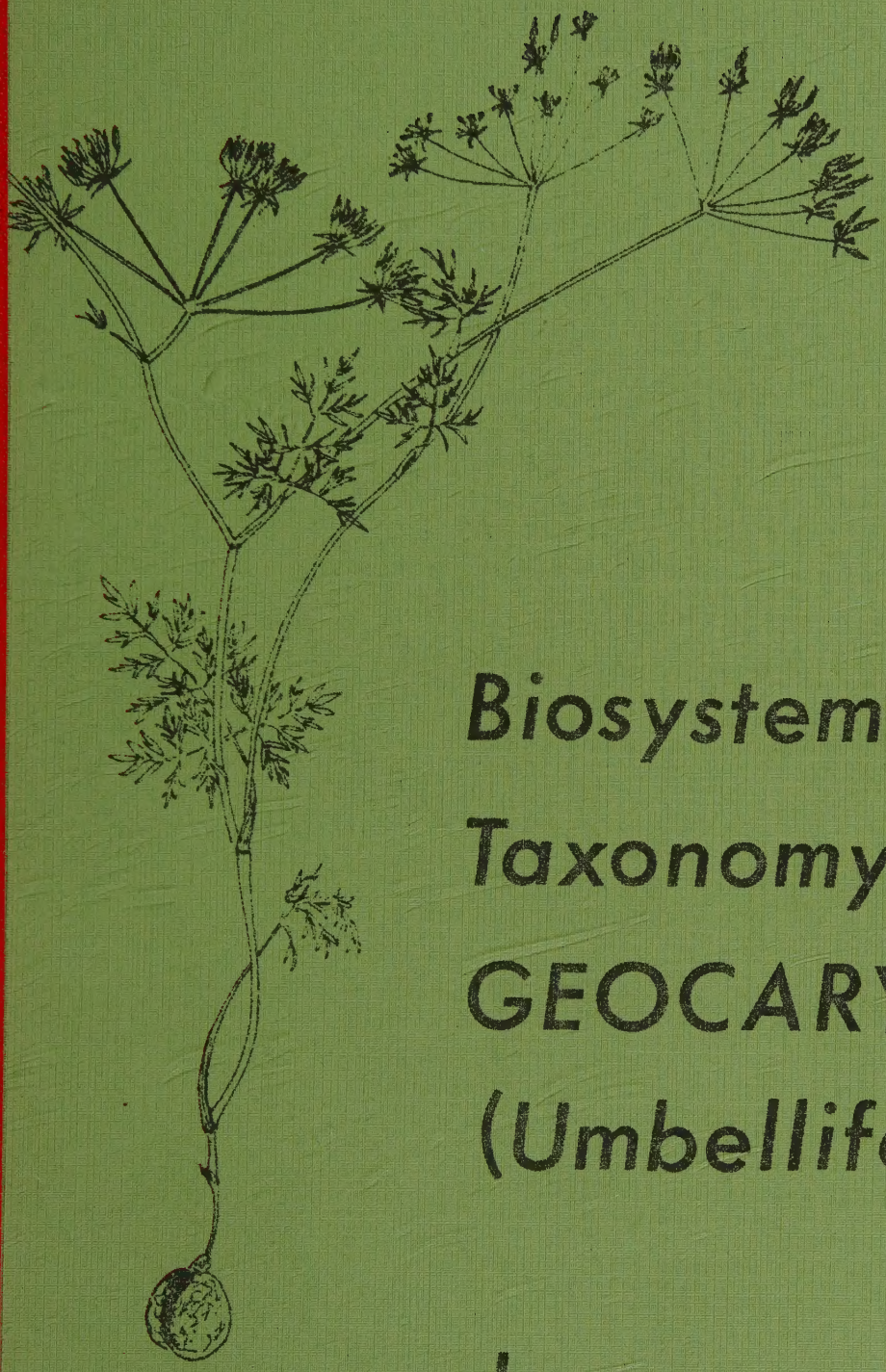

Biosystematics and Taxonomy in GEOCARYUM COSSON (Umbelliferae)

by

Lennart Engstrand

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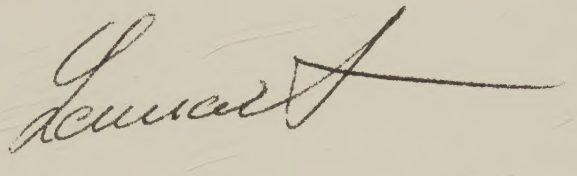
Jag vill säga ett varmt tack till alla dem som hjälpt mig med arbetet med "dom där knölumbellaterna". Hjälp och stöd har jag fått i många former. Det har gällt t.ex. diskussioner, anskaffning av material, undervisning i metodik, laboratoriearbete och odling. Under de sista månaderna har jag fått ovärderlig hjälp med utskrivning, manuskriptläsning, språkgranskning, stencilering och andra tekniska svårigheter.
Ett uppriktigt tack är alltså välbefogat.



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BIOSYSTEMATICS AND TAXONOMY IN GEOCARYUM Cosson (UMBELLIFERAE)

BY LENNART ENGSTRAND

ENGSTRAND, L. 1977, BIOSYSTEMATICS AND TAXONOMY IN GEOCARYUM COSSON (UMBELLIFERAE)

The genus Geocaryum Cosson (Huetia Boiss.), Umbelliferae, has been the subject of: (1) A general morphological study. (2) A taxonomic revision. (3) A biometric study of morphology. (4) A study of biochemical variation by means of thin-layer chromatography (extractable in HCl-metanol). (5) A cytological study. (6) Crossing experiments. Thirteen species are recognized of which G. peloponesiacum is new. The breeding system, variation pattern, speciation and different modes of diversification are discussed. The differentiation of the genus is found to be of considerable age and the modes of evolution are summarized under three points: Formation of tetraploids and aneuploids, adaptation through the formation of ecotypes and vicariance. The species are regarded as Tertiary relicts. Five species are local insular or montane endemics. All species are predominantly autogamous and characterized by genetic stability.

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I. INTRODUCTION

GENERAL SURVEY

Geocaryum is a genus of apioid Umbelliferae, distributed in S Italy, the Balkan Peninsula, some of the islands of the Aegean Sea and in W and S Turkey. The species are montane or alpine, in only a few localities having been found below 500.

Geocaryum is closely related by Bunium and Conopodium. The three genera have in common a subterranean, globose tuber, pseudomonocotyledonous embryos and display similarities in fruits and vegetative parts. Geocaryum is, however, easily distinguished by small papillae on the fruit surface visible at a magnification of 10 times.

The circumscription and nomenclature of the genus has been somewhat confused. The circumscription has already been treated by the author (Engstrand 1973). The taxonomy has been dealt with by Ball (1968 a) who recognized three species, one of which he split up into three subspecies. Ball considered the Sicilian material belonged to Conopodium (Ball 1968 b).

Other comprehensive works on the genus are by Boissier (1872), Hayek (1927) and Halácsy (1901).

The present study forms part of a research programme initiated by Runemark in 1957 to investigate the evolutionary patterns in especially small population systems in the Aegean area. Other published works in the project are Heneen &

Runemark (1962, 1969, 1972 a,b), Snogerup (1967 a,b), Strid (1969, 1970), Stork (1972), Bentzer (1973), and von Bothmer (1974).

AIMS, METHODS AND MATERIAL

Aims: (1) To investigate intra- and interpopulational variation. (2) To elucidate possible ways of differentiation. (3) To provide an acceptable taxonomic subdivision of the genus.

Methods: (1) A general morphological study. (2) A biometric study of morphology. (3) A study of biochemical variation by means of thin-layer chromatography. (4) A cytological study, mainly by means of determinating the chromosome numbers. (5) Cultivation experiments.

Material: Material from the following herbaria has been investigated: BM, COI, E, FI, G, K, L, LD, LISU, LY, MA, P, S, UPS, W, WU. (Abbreviations according to Lanjouw & Stafleu 1964). Living material, grown mainly from tubers collected by the author and his colleagues has been raised in greenhouses and outdoors at the Botanical Garden, Lund. A list with the origin of the cultivated material is given in the appendix.

ETHNOBOTANY

According to unverified reports the subterranean tubers of Geocaryum were formerly eaten by Greek peasants. This seems likely as the related Bunium bulbocastanum has been cultivated for its edible tubers. According to Hegi (1926) Bunium ferulaceum has been eaten but to my knowledge it has never been culti-

vated, Tubers of Geocaryum are also said to have been eaten by women to ensure that they have male children.

SPECIES RECOGNIZED

The Aegean group

G. macrocarpum	2n=20	Greece: Attiki, Aegean islands; SW and S Turkey.
G. stylosum	2n=20	Greece: Samos; W Turkey.
G. bornmuelleri	-	Greece: Thasos.

The pumilum-pindicola complex

G. pumilum	2n=20	Greece: Mt Parnassos.
G. peloponesiacum	2n=20	Greece: Peloponnisos, Kefallinia.
G. creticum	2n=20	Greece: Crete.
G. pindicola	2n=20	S Albania; C Greece.

The Adriatic group

G. cynapioides	2n=18	Italy: Abruzzi.
G. tuberosum	2n=18 (0-4)B	Yugoslavia and Albania: The E Adriatic coast.

The capillifolium group

G. capillifolium	2n=10,20 (0-9)B	Italy: Sicily and S mainland; S and E Yugoslavia; W Bulgaria; N and C Greece; E and N Albania?
G. parnassicum	2n=10	S Greece.

Dubious species

G. euboicum	-	Greece: Euboea.
G. divaricatum	-	Greece: Mt Killini.

II. MORPHOLOGY AND GENERAL DESCRIPTION

HABIT AND STEM

Habit

The material can be divided into erect species and more or less procumbent species. This division does not entirely coincide with the subgroups of the genus and in some species single individuals may deviate. These two types of habit are adapted to special habitats and have proved to be constant in cultivation though the height of the plants and the length of the underground parts may be modified.

(1) Procumbent species: The pumilum-pindicola complex, viz. G. pumilum, G. peloponesiacum, G. creticum and G. pindicola, but also G. macrocarpum in the Aegean group. Single individuals of G. pindicola and G. macrocarpum can be more or less erect.

In the procumbent plants both internodes and branches are curved. The species are much branched and secondary and even tertiary branching may occur. In some species the branches can form an angle of up to 180^{o} with the stem. The underground part of the stem is long and flexuous. The plants inhabit screes and other stony places.

The tubers are situated c. 5--15 cm below the soil surface, where there is an accumulation of mineral particles and organic matter. The length of the underground part of the stem is modified depending on edaphic conditions.
(2) Erect species: G. stylosum, G. bornmuelleri, G. tuberosum, G. cynapioides, G. capillifolium, G. parnassicum, G. euboicum, G. divaricatum.

Internodes and branches are straight but G. parnassicum deviates more or less in this respect. They are little branched, usually one or two, rarely more, secondary branches are rare; axils 40^{o}--60^{o}. The species inhabit mountain forests or meadows where there is no shortage of organic matter in the surface layer. The tubers are situated just below the surface so that the underground part of the stems is usually one or a few cm long. G. stylosum, G. parnassicum and probably also G. divaricatum sometimes have longer underground stems depending on the edaphic conditions.

Anatomy of stem

Below the epidermis, consisting of a single layer of cells, are collenchymatous ribs alternating with chlorenchyma giving the stem a striate appearance, and below the ribs are vascular bundles. Between the phloem and the collenchyma oil ducts are embedded in thin-walled cortex cells. The xylem is surrounded by sclerenchyma which forms an umbroken layer around the stem. The number of collenchymatous ribs and consequently also the number of vascular bundles varies, usually 15--25, some being more prominent than others. The parenchymatous pith sometimes breaks down so that the stem becomes hollow.

LEAVES

The leaves are triangular in general outline. They are not truly pinnate

but as this term is commonly used in the description of Umbelliferae leaves it is also used here.

There is a gradual change in the division and shape of the lobes from below upwards. The basal leaves originate from a part of the stem just above the tuber with very short internodes so that the petioles of these leaves are underground. In plants where the tubers are situated deeper in the ground the laminae may be up to 10 cm from the stem. The basal leaves are 2--4-pinnate with short lobes.

In cauline leaves (above the surface) the petioles tend to be shorter, the upper cauline leaves consist of an undivided, filiform lamina or a leaf sheath only.

The leaf lobes usually have small, unicellular hairs along the margins (see Fig. 4). These may occur irregularly in the species and the size may vary. In G. cynapioides they are always present in several rows along the margins and also along the midrib under surface.

INFLORESCENCE AND FLOWER

Inflorescence

As in other apioid Umbelliferae the flowers are arranged in compound umbels with primary and secondary rays. The number and length of the primary rays are constant within a species and have also proved to be so in cultivation (see VI. Morphological variation). The three northern erect species do not have the similar curvature of the rays. Those of G. cynapioides are almost straight, so that the umbel resembles a broom. In G. tuberosum the rays are uniformly bent upwards while in G. capillifolium (both cytotypes) the rays are bent twice, first outwards and then upwards, which makes them look like a swanš neck (Fig. 3).

The umbels of secondary and tertiary branches usually have more rays than the terminal one but there is also a higher per cent of male flowers. Bracts are found only as rare exceptions but bractlets are always present. For the number and shape of bractlets see part VI. Morphological variation.

Flower

Both male flowers and perfect ones occur. Staminate flowers with very small styles and rudimentary ovaries sometimes occur, but have never been observed to develop into perfect functional ones. However, it is not impossible that such flowers in secondary and tertiary umbels can be developed if the terminal umbel is damaged. Normally the terminal umbel produces by far the greatest numbers of seeds. The diameter of a male flower is usually less than that of a perfect one.

The petals are ovate or obovate but as the acute apex is inflexed they appear obcordate. They are white or rarely somewhat pinkish with a prominent midrib. On both sides of the midrib there are stomata.

The stylopodia are shaped like cupolas or low cones. The colour is green in the Aegean species and the Adriatic group, viz. G. macrocarpum, G. stylosum, G. bornmuelleri, G. cynapioides and G. tuberosum. The stylopodia are white in the pumilum-pindicola complex and in the capillifolium group. The colour can only be observed in flowering individuals and consequently nothing is known in G. euboicum and G. divaricatum.

At the time of flowering a thin film of nectar covers the stylopodium. On the surface of the stylopodium are pores shaped like the funnels of old-fashioned gramophones. At the bottom of the funnel is a thick-walled cell, which most certainly is responsible for the nectar production (Fig. 4). The opening of the funnel is 14--22 µm in diameter and at the bottom 7--14 µm. The pore is 6--14 µm deep. The same type of nectar-producing organs were found in Scaligeria halophila (Rech. fil.) Rech. fil, but the funnels there are larger.

The diameter at the top is 30--37 µm, and at the bottom c. 20 µm. The pore depth is 10--16 µm. Little seems to be known about the secretory cells of stylopodia in Umbelliferae. In Conium maculatum L. Bell (1971) found a subepidermal layer which he presumes is nectar producing. In some species of Angelica he mentions "pits" on the surface which seem to be centres of nectar secretion.

The two styles are pressed together at an early stage of anthesis but usually diverge later. They are whitish and, in the species with green stylopodia, have a green base.

The stamens are 5 with dorsifixed anthers. They are arranged in one plane but open in an order which indicates a 2/5 spiralization. In the species G. pumilum, G. peloponesiacum and G. creticum the anthers are dark red. G. stylosum has pink anthers, while G. macrocarpum has pink or greenish-white ones. In all other species seen in flower the anthers are greenish-white.

MATURE FRUIT, STYLE AND STYLOPODIUM

Fruit characters are of taxonomic importance in the Umbelliferae enabling the family to be split up while still keeping the genera rather constant. However, it has recently been found that similar fruits are not necessarily the result of similar types of development (Theobald 1971). This fact dimishes the value of the fruits in this aspect. The value of the fruits for generic delimitation in Bunium, Conopodium and Geocaryum has already been discussed (Engstrand 1973). The constancy in fruit characters in Geocaryum indicates that the genus is homologous and well defined.

The schizocarp is composed of two more or less unspecialized mericarps. In lateral view the fruit is linear-oblong, somewhat narrowed in the upper part. The length is 2.7--6.5 mm, style and stylopodium excluded, the width c. 2 mm.

Especially in species with the higher chromosome numbers there is a distinct constriction below the stylopodium. The beak is, however, never so distinct as in Anthriscus cerefolius or Scandix, for example.

Each mericarp has five prominent ridges (jugae) each with a schlerenchymous bundle, sometimes with a minor oil duct external to it. In each vallecula is one vitta and on the commisural face usually two. However the vittae are often all absent at maturity.

The sharpness of the ridges is a good indication of the chromosome number. In diploid plants the ridges are not so high and sharp as in those with higher chromosome numbers where the epicarpal cells are fan-shaped in transverse section just at the top of the ridges (Fig. 4). In part of the G. pumilum material there are small tubercles or teeth along the ridges (see VI. Morphological variation).

The fruit surface is covered by a cuticular structure of small papillae, visible at a magnification of 10 times (Engstrand 1973 Fig. 2 A).

The mature fruits are black or brown-black, sometimes very dark greenish-black.

The shape of the mature style and stylopodium has proved to be of some taxonomic value. During the process of maturation the central part of the stylopodium sinks down and the periferal part forms a collar around the styles. The collar is best developed and most distinct in the species of the Aegean group, viz. G. macrocarpum, G. stylosum and G. bornmuelleri. However, it is also plainly visible in the other species.

The two dry styles of a fruit are usually slightly divergent but in G. creticum they are curved backwards. In G. euboicum and in the Parnis and Imittos material of G. macrocarpum the styles are bent abruptly backwards forming an angle of about 90^{o} with the mericarps.

GERMINATION

Seeds collected in nature during the summer of 1968 were sown in 278 pots in October and placed in greenhouses. The seed material represented 278 individuals from the collections E1--E27, altogether c, 7000 seeds. In March 1969 a single seed from E8 (Rodhos) germinated. On 1st September 1969 the pots were divided into three groups and kept under different conditions:

(A) Refrigerator (c. +4°C).

(B) Greenhouse (+15°--20°).

(C) Outdoors (the main group).

The pots were moved from the refrigerator to the greenhouse after 1, 2, and 3 months.

At the beginning of December seeds from group (A) and (B) started to germinate. However, these all proved to be from the Aegean collections E1, E2, E3, E6, E7, E8, and E10, none from the alpine or montane collections.

In the middle of April 1970 seeds kept outdoors during the winter started to germinate. Within c. 2 weeks some seeds at least from almost all collections had germinated, including some from the Aegean area and from higher altitudes. Within 14 months from sowing seeds had germinated in 112 of the pots.

As regards germination Geocaryum can be divided into two groups:

(1) The Aegean group.

Seeds from this group germinated independent of treatment. Those kept in a refrigerator germinated at the same time as those kept in a greenhouse all the time. The seeds which were kept in the refrigerator for three months were naturally delayed for a few weeks. Seeds kept outdoors during the winter germinated early in the spring.

(2) The alpine and montane group.

Seeds from this group germinated after a long period of exposure to low temperatures. Three months in a refrigerator at +4°C was not enough. The southern Swedish winter that was needed to break the delay usually has a low

temperature at night, but often a temperature above freezing-point in the daytime.

There are too many uncontrolled factors, such as light and amount and fluctuation of water supply, to allow any definite conclusions to be drawn from this experiment. However, it is evident that plants from higher altitudes need a long period at low temperatures or perhaps fluctuations in temperature before germinating. The length of this period should prevent the onset of germination too early in spring when the risk for temperatures below $0^{o}C$ is still great.

Seeds of plants from the Aegean area started to germinate after a given time independent of the various treatments in this experiment under favourable external conditions. The shortest time needed was 13 months. If this is the case under natural conditions the seeds would germinate in the middle of the summer when the water supply in the Aegean area is very poor. A more appropriate time would be 8--9 months or possibly 20--21 months.

The problems connected with germination in Umbelliferae have been observed by many authors (e.g. Chuang & Constance 1969, Schulz-Gaebel 1930, Cerceau--Larrival 1962). The problem has been dealt with in several studies, especially on cultivated Umbelliferae where poor germination is of great economic importance. According to Robinson (1954) the recalcitrance is due to three factors: (1) Embryoless seeds as a result of an attack of the Lygus bug. (2) Rudimentary seeds where the embryos are usually in different stages of development. (3) Dormancy which has to be broken by various treatments with light and temperature. Stokes (four papers 1952--1953) has demonstrated that in seeds of Heracleum sphondylium cold treatment promotes the hydrolysis of endosperm proteins into aginine and glycine. These two amino-acids are necessary for the nutrition of the embryo during germination.

As a result of the experiment the delayed germination in Geocaryum cannot categorically be brought to only one of the three groups. In the case of the

high montane plants dormancy is probably the main cause, but rudimentary embryos would not have been revealed with the method used. As a matter of fact Haccius (1952) found seeds with unevenly developed embryos in Huetia balcanica (=G. capillifolium).

For the seeds from the Aegean plants it cannot be that type of dormancy which has to be broken by cold treatment. Rudimentary seeds may well occur, but in this case the simultaneity must either be that embryos from all seeds are in the same stage of development or that fully developed embryos had been accumulated for a certain time and still needed suitable conditions of light or some other uncontrolled factor.

Rudimentary seeds with embryos at different stages of development should be of value for a plant. In a seed pool some seeds at least will germinate under the most favourable conditions.

Experiments were also made with mechanical and chemical treatment to injure the seed coat (for the methods see Björkqvist 1967). None of these experiments resulted in germination.

THE SEEDLING

Geocaryum is pseudomonocotyledonous, a character which it shares with some other umbelliferous plants such as Bunium, Conopodium, Scaligeria and Erigenia, (cf. Weisse 1930, Haccius 1952). The phenomenum is also found in other families such as Ranunculaceae, Papaveraceae, Primulaceae, Portulacaceae, Celastraceae and Asteraceae (Weisse 1930).

The pseudomonocotyledonous embryo of Geocaryum was first noted by Domin (1908). Hegelmaier (1878) treated the germination of Bunium bulbocastanum which seems to be similar to that of Geocaryum. Hegelmaier (1878) stated that Irmisch (1854) studied Geocaryum creticum (Butinia cretica) but this is a

misunderstanding arising from the nomenclatural difficulties in Scaligeria and Geocaryum (Engstrand 1970). Irmischs drawings clearly show the cotyledon of Scaligeria napiformis (Sprengel) Grande. The most detailed study of the germination of Geocaryum is that of Haccius (1952).

The seedling can sometimes become up to 23 cm long but is normally between 10 and 15 cm. The cotyledon is up to 3 x 45 mm and linear (Fig. 1) narrowing gradually downwards into the subterranean parts. The tuber becomes visible within 30 to 60 days after germination as a thickening on the seedling.

Morphologically and anatomically the seedling consists of four different parts (Fig. 2).

(1) The cotyledon with the cotyledon stalk.

This part has stomata, even on the colourless subterranean part. It has a central compressed vein and two lateral veins. The lower part is more or less elliptical in transverse section.

(2) The rest of the seedling down to the tuber.

The transition between this part and the first one is very abrupt but can be difficult to see in fresh material becoming distinct, however, after fixation This part is circular in transverse section. It has only one central vein and carries root hairs but has no stomata.

(3) The tuber.

The tuber is more or less ellipsoidal when young, but later usually becomes globose. At the top of the tuber, lateral to part (2), the opening of the plumule is visible as a small horizontal split.

(4) The primary root.

The primary root is circular in transverse section, has one central vein and carries root hairs.

It is rather difficult to find which parts of the seedling of Geocaryum that are homologous with a more usual one, e.g. of Daucus carota.

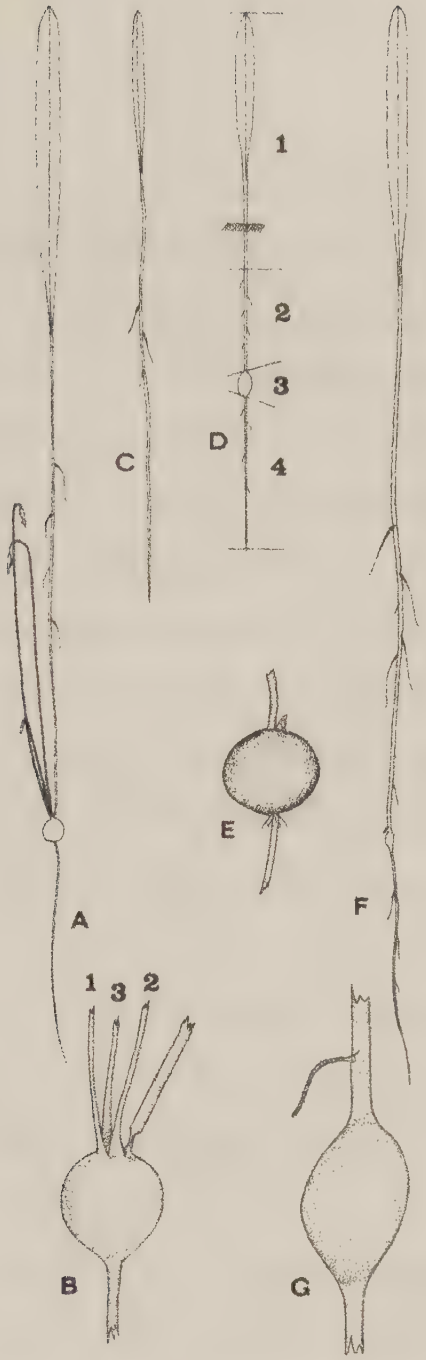


Fig. 1. Seedlings of Geocaryum. -- A: G. macrocarpum from Pelagos (E10) with three leaves developed 58 days after germination. -- B: Detail of A with the leaves numbered in the order of development. To the right is the lowest part of the cotyledon stalk. -- C: G. macrocarpum from Rhodos (E8). No tuber has developed after ca. 30 days. -- D: Schematised drawing of a seedling with the different parts mentioned in text. Surface of ground indicated. -- E: G. euboicum (E9) with the first leaf visible. -- F: G. macrocarpum from Pelagos (E10) 37 days after germination. -- G: Detail of F. -- A, C, F: X1. -- B: X8. -- E: X5. -- G: X20.

Haccius & Reh (1956) have demonstrated a transitional series of Umbelliferae seedlings from Bupleurum rotundifolium to Chaerophyllum bulbosum with an increasing degree of gamocotyly. The two cotyledon stalks are united to form a tube around the plumule, which is situated progressively lower down as the hypocotyl becomes progressively shorter. The seedling of Chaerophyllum bulbosum in principal resembles that of Geocaryum but has two cotyledons. In this way the second part in the description above must coincide with the lowest part of the cotyledon stalk. One must accept the fact that the cotyledon stalk can carry root hairs and show other great similarities with the primary root. This theory is accepted by both Velenovský (1907) and Haccius. It should be noted that the second part is positively geotropic, this possibly serving to push the tuber downwards.

According to Velenovský (1907) the tuber originates from the hypocotyl, a fact which Haccius regards as questionable. She points out that the series is characterized by a diminishing of the hypocotyl and that it should be almost totally reduced at the end of the series.

Hypothetically there are two ways for one cotyledon to be derived from the presumably two original cotyledons. The two cotyledons could be united along their total length. This theory was supported by Géneau de Lamarlière (1891). In this case it should be possible to trace the second cotyledon in an embryonic stage. However only one cotyledon develops in the embryo (Haccius). The most probable theory is that the second cotyledon becomes totally reduced, which is supported by anatomical features (see Fig. 2).

In cultivation no leaves are normally developed during the germination season. Only in plants from the collection E10 (Pelagos) can up to three leaves be present and in one case a plant even flowered without any resting period. Seedlings of G. euboicum indicated development of leaves without a resting period but unfortunately all died after a short time. In the greenhouse

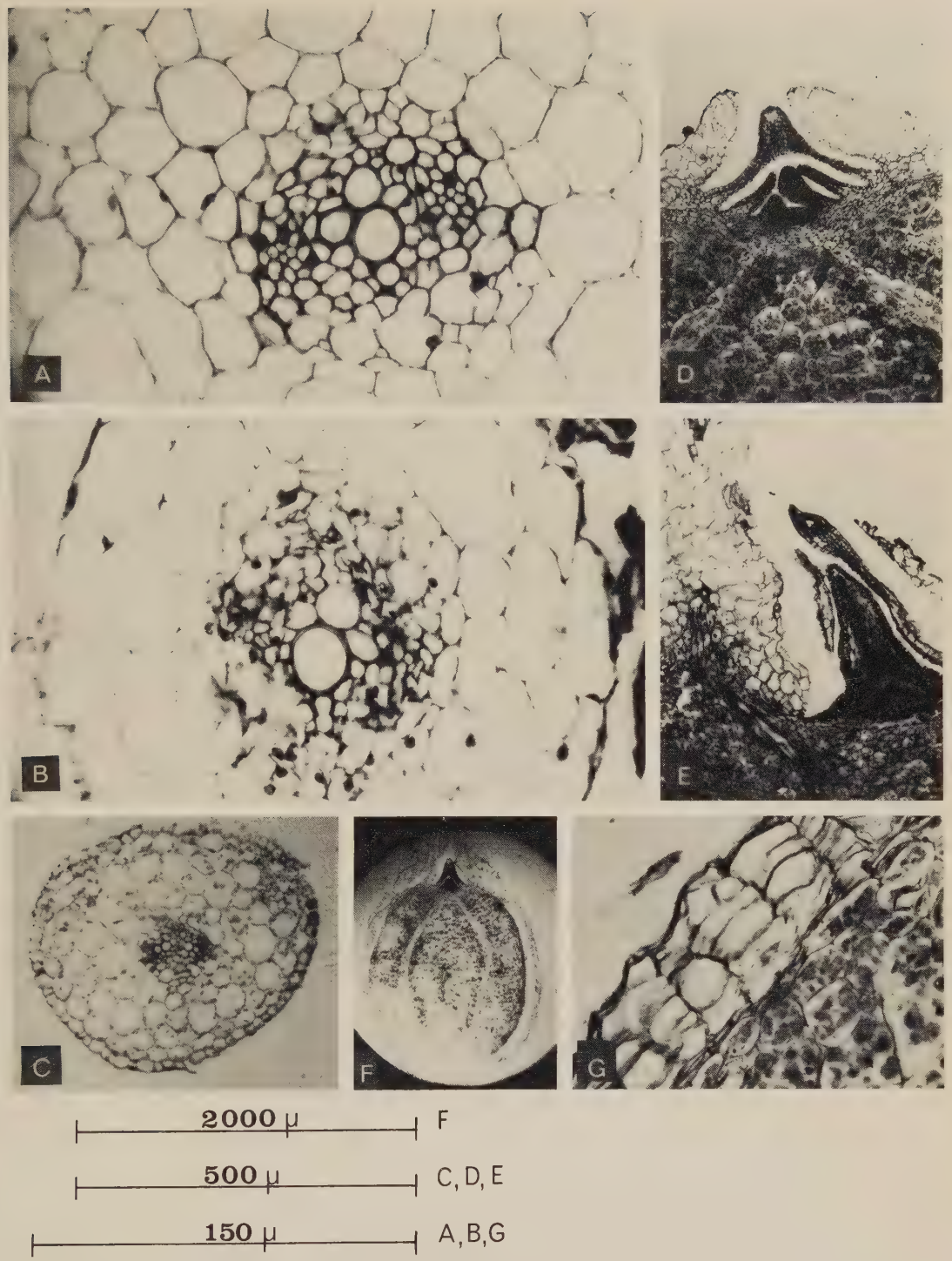


Fig. 2. Seedlings of *Geocaryum*. – A: *G. euboicum*. Transverse section of the lower part of the cotyledon stalk (part 2, see Fig. 1D). – B: *G. euboicum*. Transverse section of the primary root (part 4). – C: *G. euboicum*. Transverse section of the cotyledon (part 1). – D: *G. capillifolium*. Longitudinal section of the upper part of the tuber showing the first three leaves. – E: *G. euboicum*. Longitudinal section of the upper part of the tuber showing the first two leaves and, to the left, the lower part of the cotyledon stalk. – F: *G. capillifolium*. Longitudinal section of the tuber. – G: *G. euboicum*. Longitudinal section of the tuber showing the phellem cells.

tubers have been shown to have a duration of at least 11 years. During the resting periods the leaves, shoots and roots became totally desiccated.

POLLEN GRAINS

Background

The shape of pollen grains has proved to be of taxonomic importance in Umbelliferae. The basis for the practical work was provided by Cerceau-Larrival (1962) who has defined seven diagnostic characters visible under the light microscope, (l.c. pp. 94--96). An investigation of the different species of Tordylium L. was made by Runemark (1968 b) who stated that it is possible to distinguish all five Aegean species on the pollen grains only. These facts have been the motive for a study of pollen grains in Geocaryum.

The nomenclature follows that of Erdtman (1969) and Cerceau-Larrival (1962).

The investigation was carried out on both fresh and dry material, either unstained or stained with cotton blue or a weak solution of acetorcein. The unstained pollen was kept in Water Solution Medium.

Description of pollen grains

The pollen grains are tricolporate and isopolar. In lateral view, with one aperture exactly upwards, they are oblong, although sometimes slightly constricted in the equatorial plane (Fig. 3).

In polar view the grains are almost circular in the equatorial plane and rounded triangular away from it.

Under the light microscope the tectum of dry pollen grains is seen to be rugose. The sexine is tectate and between the colpi is thickened to form three longitudinal, low and rounded ridges which narrow abruptly near the equatorial

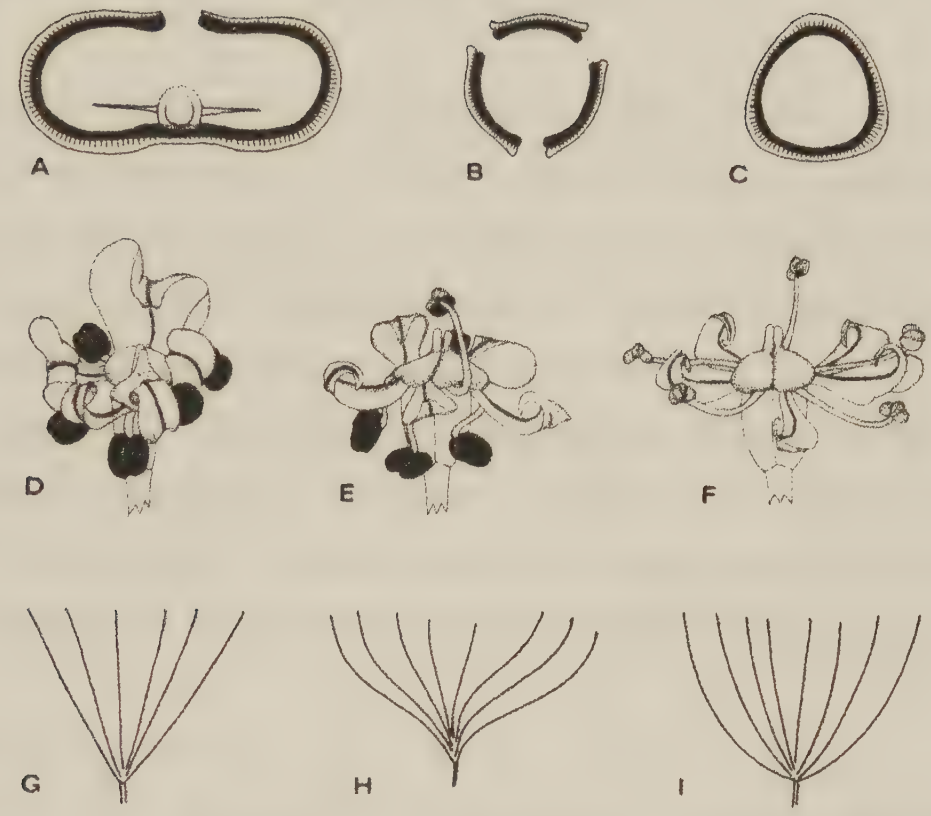
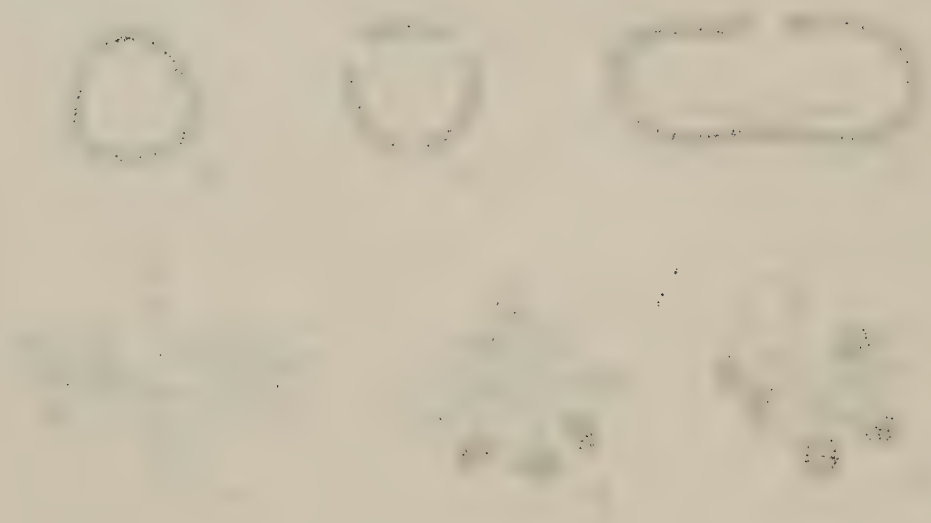


Fig. 3. A -- C: Pollen grains as seen in light microscope. -- A: Longitudinal section. -- B: Transverse section of the median part. -- C: Transverse section of the distal part. -- D -- F: The movement of the anthers during anthesis in G. macrocarpum (X9). -- D: Coll. E10. -- E: Coll. E7. -- F: Coll. E1. -- G -- I: Schematical drawing of the shape of umbels in the northern erect species. -- G: G. cynapioides. -- H: G. capillifolium. -- I: G. tuberosum.



zone. In plants with 2n=10 these ridges are not so high and consequently do not narrow so abruptly. At and near the poles the sexine is of uniform thickness.

By contrast the nexine is not so easy to observe. However, in non-viable pollen grains (not stainable in cotton blue) the nexine is usually distinct. When stained with acetorcein it is greenish in certain microscope light. The nexine is approximately of equal thickness all around, except between the colpi in the equatorial zone where it is distinctly thicker.

The ectoaperture is only seen as a longitudinal furrow reaching half-way to the poles. The endoaperture is in shape a rounded square. The sexine is bent outwards forming a wall structure around the endoaperture. The different species of the genus do not differ in the arrangement of the apertures.

Size of pollen grains

Length and width were measured on fresh pollen from cultivated material. The grains were stained with cotton blue. Measurements indicated that there is very little variation in size of pollen grains in one individual. Therefore the number of measurements was restricted to five grains per plant. Maximum, minimum and mean values from the collections investigated are shown in Table 1. The extreme values presented are the mean values of the five measurements per plant.

The ratio length/width varies from 2.0 to 2.6. These are however, single extreme values. Normally the ratio varies between 2,2 and 2.4.

There is no significant difference in length of pollen grains between species with the same chromosome number nor between species with 2n=18 and 2n=20. Grains from diploid plants are considerably smaller, the length varying from 21.7 μm to 23.3 μm. The total variation in plants with 2n=18 and 2n=20 is 24.4--34.0 μm. There is overlapping in some individuals but never in the mean

Table 1.

Length and width of pollen grains from fresh material. Min. and max. are the mean values from five measurements per individual.

Species	Coll. nr.	Length in microns M	Min.	Max.	Width in microns M	Min.	Max.	n
stylosum	E66	28.3	26.7	30.0	11.8	11.2	12.7	23
	E67	27.5	26.0	28.7	11.4	10.6	11.9	17
	E68	27.4	27.1	27.7	11.5	11.3	11.6	2
pumilum	E26	28.5	27.7	29.6	13.1	11.9	14.8	6
	E27	29.8			11.5			1
peloponesiacum	E12	27.7			11.6			1
	E13	27.3			11.3			1
	E14	26.0	25.4	26.9	11.8	11.5	12.3	3
	E15	26.2	25.2	28.8	11.9	11.5	12.3	3
	E16	28.5			11.7			1
	E17	28.1	26.2	30.6	12.4	11.5	13.3	8
	E55	27.6	27.1	28.1	12.3	11.9	12.7	2
	E62	33.8			15.4			1
creticum	E19	27.7			12.3			4
pindicola	E21	27.5	26.0	29.4	12.1	11.7	12.7	4
	E22	26.7	25.0	28.7	11.6	11.3	11.9	6
	E24	27.5	26.5	29.4	12.0	11.7	12.5	4
	E25	25.4			11.3			1
cynapioides	E44	26.9			12.3			1
tuberosum	E52	28.2	25.4	34.0	12.2	11.5	14.0	9
	E53	27.8	25.4	29.4	12.1	11.0	13.7	10
capillifolium,2n=10	E11	24.2			9.8			1
	E23	24.9	24.8	25.0	10.0	9.8	10.2	2
	E46	23.4	22.5	25.2	10.2	9.6	11.5	5
	E47	22.9			9.6			1
	E51	23.8	23.5	24.0	10.0	10.0	10.0	2
capillifolium,2n=20	E48	25.3	24.4	26.2	11.5	11.3	11.6	2
	E49	26.8	25.4	29.2	10.7	10.4	11.5	11
	E50	26.3	25.4	27.1	10.9	10.8	11.0	2
parnassicum	E5	24.0	21.7	26.3	10.5	9.8	11.0	6
	E58	25.0	25.0	25.0	10.5	10.4	10.6	2
	E61	22.7			11.2			1
	E63	23.5			9.6			1

Table 2.
Size of pollen grains compared with chromosome number. A summary of Table 1.

Chromosome number	Length in microns			Width in microns			n
	M	Min.	Max.	M	Min.	Max.	
2n=10	23.9	21.7	26.3	10.2	9.6	11.5	21
2n=18	27.9	25.4	34.0	12.2	11.0	14.0	20
2n=20	25.9	24.4	30.6	11.8	10.4	15.4	100

values of collections. The differences are very pronounced. Thus size of pollen grains and the chromosome number is well correlated (Table 2). In the mainly N American genus Perideridia Chuang and Constance (1969) found that this correlation was by no means constant.

Summary

The morphology of pollen grains is in accordance with the general morphology of the family which was described by Erdtman (1952). The morphological variation in the genus is very small compared with that of Tordylium.

The size of grains varies little in one individual but there is considerable variation between individuals from the same population. With this background the material must be considered too limited to indicate any differences between species with the same level of ploidy. Pollen grains from plants with 2n=10 are distinctly smaller than those from plants with 2n=18 and 2n=20.

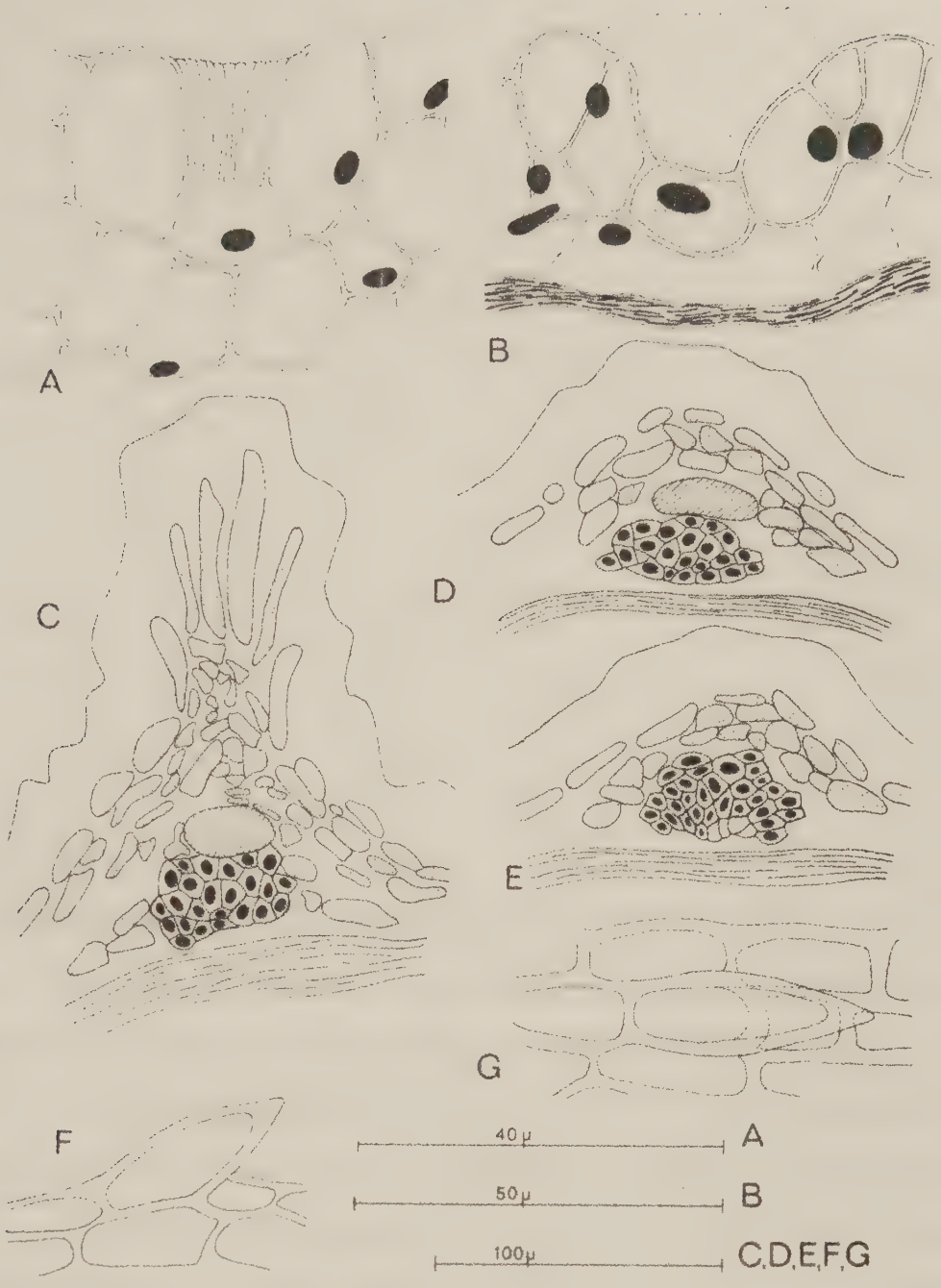


Fig. 4. A: G. macrocarpum (E6, Imittos). Transverse section of the nectar producing organ of the stylopodium. -- B: Scaligeria halophila (Rech. fil.) Rech. fil.. Transverse section of the nectar producing organ of the stylopodium. -- C: G. tuberosum (E52). Transverse section of a lateral ridge of a mature mericarp showing the prolonged cells of the epicarp. -- D: G. capillifolium (E51). Same as C but the cells are not prolonged. -- E: G. capillifolium (E45). Same as D but the oil duct is missing. -- F: G. capillifolium (E51). One celled hair of a leaf lobe seen from the side. -- G: G. capillifolium (E51). One celled hair of leaf lobe seen from above.

III. TAXONOMY

TAXONOMIC DIFFICULTIES

The genus Geocaryum consists of a number of populations which grow on mountains or islands. Thus they are very effectively isolated from one another. In some cases there are two or even three species on the same mountain but in this case the chromosome numbers differ and/or they are found growing in different habitats, which obviously also makes the isolation quite effective. As populations are often morphologically unique and distinct from all other populations and hybrids are not found many populations can be regarded as separate taxa, even as species. They are morphologically distinguishable with discontinuities in several characters and are genetically isolated. If all these forms were described as taxa it would be very impractical as the great number of taxa would totally mask the evolutionary pattern of the genus. Thus discontinuities at a higher level must be looked for to delimit acceptable species. It is necessary to ignore the fact that the taxa do not function as biological units.

Geocaryum has been divided into three types of species: (1) Species consisting of several populations but still fairly uniform and not difficult to circumscribe. (2) Species consisting of several populations but with a wide and

discontinuous variation and difficult to circumscribe. (3) Species consisting of one or few populations and consequently easy to circumscribe.

To the first group belong G. stylosum and G. macrocarpum. They are fairly homogeneous and there is no difficulty in delimiting them. G. pindicola is a representative of group (2). It is very variable in traditionally important characters such as length of rays and leaf lobes and presence or absence of teeth at the apex of the pedicels. At maturity it may be difficult to distinguish it from G. peloponesiacum. Of the local endemic species in group (3) G. pumilum is quite clear as there is a great deal of information available both from cultivation and from herbaria. As regards G. divaricatum and G. bornmuelleri it is also quite clear that they must be accorded the rank of species as each of them is morphologically unique and has only been collected once and not been refound.

Twenty-six names of varying taxonomic rank have been used within Geocaryum. When the floristic exploration of the Balkan Peninsula began it was natural to describe a newly-found population as a new taxon as it differed from all others. This of course happens in all areas where floristic exploration is going on. Ball (1968) made a very drastic reduction in the number of taxa in Geocaryum (Huetia), in part at least as only one species was considered to occur on each mountain. Consequently such great differences as those between G. divaricatum and G. peloponesiacum was regarded as being within the natural variation within a taxon (in this case between subspecies) which also applies to G. parnassicum and G. macrocarpum on Mt Parnis.

In the present taxonomic treatment of Geocaryum it must be accepted that in some cases it is impossible to give good key characters. This fact must, however, be seen against the background of the total taxonomic situation in Umbelliferae. It is obvious that it is difficult to define a number of genera and to give them good key characters as these are often only seen at a certain stage of development.

NOTES ON THE DESCRIPTIONS AND THE KEY

The stem measurement also includes the underground part. The word pinnate has been used of the leaves even when they are not truely pinnate. The primary divisions are referred to as segments and the ultimate divisions as lobes. The word bractlets has been used instead of the more commonly used bracteoles. It is regarded as a diminutive form of bract.The small unicellular teeth at the apex of pedicels are observable at anthesis but are more easily seen at maturity. The length of the fruits does not include the style and the stylopodium.

Measurements within parentheses have no exact statistic meaning mainly because the material is often limited. They have been selected more or less subjectively in order to indicate some extreme values of variation. Sometimes the values of variation are followed by e.g. "usually one or two". This method of description has been used when some values have been considered to be very typical for a species, or can be of great help in the work of determination.

GEOCARYUM COSSON EMEND. ENGSTRAND

Cosson 1851 p. 112. -- Biasolettia Koch 1836 p. 163 (type Biasolettia tuberosa Koch), non Biasolettia Presl 1835. -- Freyera Reichenbach 1837 p. 291 (type Freyera tuberosa (Koch) Reichenbach , orthographic variant of Freyeria Scopoli 1777. -- Huetia Boissier 1856 p. 103 (type Huetia pumila (Sibth. & Smith) Boissier & Spruner).

Type: Geocaryum capillifolium (Gussone) Cosson.

Comments: The confused history of the nomenclature of Geocaryum is presented in Engstrand (1973), where the generic delimitation of Bunium, Conopodium and Geocaryum is also given. There is no difficulty in defining the genus but in

practice Geocaryum has often been confused with specimens of Bunium and Conopodium. There are a considerable number of heterogeneous sheets in Europaean Herbaria especially as regards G. tuberosum and G. capillifolium which have been confused with Bunium species. Ball (1968 b) referred the Sicilian material of G. capillifolium to Conopodium. Sicilian material is the nomenclatural type of Cossons' name Geocaryum but he had also misinterpreted the Sicilian plant, which means that the circumscription of Geocaryum is essentially changed in my revision of the genus.

Description: Perennial. Stock a more or less globose tuber. Underground part of stem short (c. 1 cm) or long and flexuose. Stem herbaceous, erect to procumbent, terete, sometimes striate, rarely hollow. Branches none to many, sometimes with secondary branches. Leaves triangular in outline, 2--4 pinnate, the uppermost ones often undivided or only as a sheath; shape of leaf lobes filiform to linear-lanceolate to broadly elliptical to oblong, acute to subobtuse; basal leaves appear to originate from the tuber, thus with underground petioles, usually desiccated at anthesis. Outer flowers of the umbel zygomorphic, central ones more or less actinomorphic. Sepals minute. Petals first white or reddish, obcordate due to the inflexed apex. Immature stylopodium cupola-like or conical, green or whitish. Anthers dark red to pink to whitish. Bracts absent (rarely 1--5). Bractlets linear to lanceolate to oblong, acute, sometimes with a membraneous margin, sometimes ciliate or pubescent. Fruits narrowly linear-oblong, black or brownish with very small cone-shaped papillae on the surface; each mericarp with five more or less sharp ridges; vittae one per interval, often two on the commissure, rarely small interjuged ones, all sometimes lacking at maturity; mature stylopodium forming a more or less distinct collar around the styles; styles erect to divaricate. Chromosome numbers 2n=10,18,20. B chromosomes occurring.

KEY TO THE SPECIES

1a. Plant erect 2
2a. With distinct 1-celled teeth at apex of pedicels 3
3a. Fruit not more than 4.5 mm; stylopodium white at anthesis 4
4a. Upper leaf a filiform, undivided lamina, not more than 20 mm long; internodes curved; number of rays 4--7 .... parnassicum
4b. Upper leaf usually divided in filiform lobes; internodes ± straight; number of rays 5--13 ..... capillifolium
3b. Fruit more than 4.5 mm; stylopodium green at anthesis .. 5
5a. Bractlets of about the same length as fruiting pedicels; lobes of cauline leaves with numerous 1-celled teeth .. cynapioides
5b. Bractlets about half the length of fruiting pedicels; lobes of cauline leaves with few or none 1-celled teeth.tuberosum
2b. Without teeth at apex of pedicels 6
6a. Lobes of cauline leaves at least 2.5 mm broad 7
7a. Divaricately branched; styles slightly divergent ..... divaricatum
7b. Branches lacking or 1 small branch; styles recurved ... euboicum
6b. Lobes of cauline leaves less than 2.5 mm 8
8a. Rays in terminal umbel 11 or more ..... bornmuelleri
8b. Rays in terminal umbel 9 or fewer 9
9a. Bractlets linear-triangular to narrow-lanceolate; lobes of upper cauline leaves filiform, more than 6 mm long. stylosum
9b. Bractlets ovate-lanceolate; lobes of upper cauline leaves narrow-lanceolate, usually not more than 6 mm.. 10
10a. Stem erect-procumbent, branched below the middle ... macrocarpum
10b. Stem erect, if branched then above the middle ..... tuberosum
1b. Plant procumbent 11
11a. Anthers white or pink; length of pedicels c. 4 mm or more 12
12a. Bractlets usually 5, stylopodium green at anthesis; collar of mature stylopodium conspicuous ..... macrocarpum
12b. Number of bractlets usually 2--4; stylopodium white at anthesis; collar of mature stylopodium small ..... pindicola
11b. Anthers dark red; length of pedicels c. 3 mm 13
13a. Styles backward curving; lobes of upper leaves elliptical ..... creticum
13b. Styles erect or slightly divergent; lobes of upper leaves lanceolate 14
14a. Bractlets pubescent ..... pumilum
14b. Bractlets glabrous or shortly ciliate ..... peloponesiacum

SUBGROUPS OF THE GENUS

The genus can be divided into some groups which are presumed to reflect the phylogenetic relationships of the species. However, the delimitation has been considered too weak to support a taxonomic subdivision of the genus.

The Aegean group: G. macrocarpum, G. stylosum, G. bornmuelleri.

The species are distributed in some Aegean islands, around the Aegean Sea and in S Turkey. They are erect or procumbent plants. The collar around the dry styles is conspicuous and the apex of the pedicels is not toothed. The anthers are white or pink and the stylopodium green. Chromosome number 2n=20.

The pumilum-pindicoal complex:G. pumilum, G. peloponesiacum, G. creticum, and G. pindicola. The first three species are closely related (the pumilum group) and together with the somewhat remote G. pindicola form a complex.

The species are distributed in C and S Greece, including Crete. They are procumbent montane or alpine plants. The collar around the dry styles is not conspicuous and the apex of the pedicels is not toothed or has small teeth. The stylopodium is white. Chromosome number 2n=20.

The Adriatic group: G. cynapioides, G. tuberosum.

The species are distributed in mountains on both sides of the Adriatic Sea. They are rather stout, erect species. The collar around the dry styles is not conspicuous and the apex of the pedicels is toothed (with few exceptions). The anthers are white and the stylopodium green. Chromosome number 2n=18.

The capillifolium group:G. capillifolium, G. parnassicum.

The species are distributed in mountains of the Balkan Peninsula and in S Italy, including Sicily. They are slender, erect species with straight or curved internodes. The collar around the dry styles is not conspicuous and the apex of

the pedicels is toothed (with few exceptions). The anthers are white (yellow -green) or pink and the stylopodium is white. Chromosome numbers 2n=10 and 2n= 20.

Dubious species: G. euboicum, G. divaricatum.

The species are imperfectly known and cannot be classified.

GEOCARYUM MACROCARPUM (BOISS. & SPRUNER) ENGSTRAND COMB. NOV.

Butinia macrocarpa Boissier & Spruner 1844. In Boissier Plantae Aucherianae. -- Ann. Sci. Nat. Ser. 3.2., p. 32. -- Freyera macrocarpa (Boiss. & Spruner) Boissier & Spruner 1856 p. 101. -- Biasolettia macrocarpa (Boiss. & Spruner) Nyman 1879 p. 302. -- Huetia cynapioides (Guss.) P.W. Ball subsp. macrocarpa (Boiss. & Spruner) P.W. Ball 1968 p. 16. -- Orig. coll.: Boissier, Hymettos mai 1842 (lectotype in G (Herb. Boissier)).

Biasolettia Barbeyi Freyn 1897 p. 614. -- Freyera Barbeyi (Freyn) Rechinger fil. 1943 p. 406. -- Orig. coll.: Forsyth Major 1886 (Exsicc. 577), in Insula Rhodos, 17 aprili (lectotype in G).

Freyera macrocarpa Boiss. & Spruner subsp. sporadum Phitos 1967 p. 127. -- Orig. Coll.: Phitos, Kyra Panagia: prope monasterium. Ph. 2410 (holotype in Patras).

Comments: There are two syntypes of G. macrocarpum, both in G (Herb. Boissier), one collected by Spruner and one by Boissier. They are equal and the one collected by Boissier is here chosen as lectotype. When Freyn described B. Barbeyi he was obviously not aware of the existence of G. macrocarpum as he compared the Rodhos material with all other known species of the genus but not with G. macrocarpum.

Fig. 5. Geocaryum macrocarpum. -- A: Habit (Naxos). -- B: Mericarps from (from the left): Pelagos, Naxos, Tinos, Rhodos, Mt Imittos. -- C: Fruit from Mt Parnis. -- D: Apex of pedicel with part of carpophore. -- E: Bractlets from different populations. -- F: Transverse section of mericarp (Pelagos). -- G: Sideview of stylopodia from Pelagos (to the left) and Naxos. -- A: X0.5. -- B, C, E: X8. -- D, G: X20. -- F: X40.

Description: Erect to procumbent perennial with curved stem. Tuber globose, in flowering individuals 8--28 mm in diameter. Stem 13--45 cm, glabrous or pubescent in the lower part. Underground part of stem flexuose, up to 12 cm long. Branches (1--)2--3(--4), equalling or exceeding the terminal umbel, curved; the first branch originating from the lower part of stem. Basal leaves broadly triangular in outline, 3--4-pinnate, ultimate lobes about 5 mm long, lanceolate, acute, petiole long, up to 15 cm; upper cauline leaves triangular, 1--2-pinnate, very rarely undivided, lobes lanceolate, 2--8 mm long; leaf sheaths ciliate. Number of umbels 2--4, very rarely more; terminal umbel with (3--)5--8(--11) rays; rays (12--)15--35(--48) mm long. Bracts lacking. Bractlets 3--6, usually 5, triangular to lanceolate to ovate, more often with a conspicuous membraneous margin irregular in shape, sometimes setaceous, margin usually glabrous but sometimes shortly ciliate. Petals white or reddish when young. Anthers white, greenish or pink. Stylopodium green at anthesis. Pedicels without small teeth at apex, sometimes thickened in fruit. Fruit black, linear-oblong, gradually narrowing at apex, 3.5--6.4 mm long, usually 4--5 mm, ridges prominent; styles slightly divergent or recurved; length of style and stylopodium 0.8--1.7 mm; stylopodium forming a distinct collar at maturity; vittae one per interval, more often 2 commissural ones. Chromosome number 2n=20. Illustration Fig. 5.

Flowering period: End of March to May.

Distribution and habitat: G. macrocarpum is distributed on Rodhos, SW and W Turkey, some islands of the Cyclades and the N Sporades and two mountains in Attiki. It is found from sea level to 1400 m. The lowest altitudes are found on the small islands of Pelagos and Yioura of the N Sporades and the highest on Mt Parnis in Attiki. The species is found in habitats which are sheltered in some way, on the islands often in thickets of Quercus coccifera and other macchia elements. On Tinos G. macrocarpum is found in the low spiny bushes of Sarcopoterium spinosum. On Rodhos it is found in the poor vegetation of the

Cupressus sempervirens forest and on Mt Parnis in Abies cephalonica forest. These localities are often the most protected and moistest places found in the surroundings. Plants found associated with G. macrocarpum on Rodhos (E8) are: Allium subhirsutum, Asphodelus macrocarpus, Briza maxima, Cupressus sempervirens, Pinus brutia, Poa bulbosa, Quercus coccifera, Selaginella denticulata. Associated plants from Tinos (E4) are: Allysum tenium, Anthoxantum odoratum, Briza maxima, Carex distichya, Cistus creticus, Cytinus hypocistis, Dactylis hispanica, Melica minuta, Sarcopoterium spinosum. Plants from Pelagos (E10) are: Arbutus unedo, Brachypodium ramosum, Pistacia lentiscus, Quercus coccifera, Tamus communis. (Fig. 8).

Variation and distinguishing characters: G. macrocarpum is in general habit fairly uniform but may vary in some details, e.g. shape of the bractlets, colour of the anthers and size of the fruits. Variation within each population is very slight. The populations from Attiki (Mt Imittos and Mt Parnis) are distinguished by the pedicels which are thickened in fruit and by the styles which are recurved.

G. macrocarpum belongs to the Aegean species group thus lacking teeth at the apex of the pedicels and the mature stylopodium is conspicuously collar--shaped. It is distinguished from the other species in this group, G. bornmuelleri and G. stylosum, by its lower, more procumbent habit. The stems and branches are distinctly curved.

GEOCARYUM STYLOSUM (BOISS.) ENGSTRAND COMB. NOV.

Butinia stylosa Boissier 1844. Ann. Sci. Nat. Ser. 3,2. p. 63. -- Freyera stylosa (Boiss.) Boissier 1856 p. 101. -- Orig. coll.: Boissier, Tmolos Bozdagh (lectotype in G (Herb. Boissier)).

Freyera (Biasolettia) platycarpa Huber-Morath 1945, p. 151. -- Orig. coll.: A. Huber 1938 (5589). Kleinasien; Carien, Pinus-brutia-wald Kale Tavas-Mugla, 27 km vor Mugla, 1150 m, 6.6. (holotype in Herb. Huber-Morath, Basel).

Comments: In the description of Butinia stylosa Boissier cites two collections. Possibly these two syntypes are present in the Boissier Herbarium but one is without any note of the locality and may be "Mesogis supra Tralles". The other sheet is marked Tmolos Bozdagh and is chosen as lectotype.

Freyera platycarpa is regarded as a synonym as the only character distinguishing it from collections E of Izmir and on Samos is the short hairs on the basal leaves.

Description: Erect perennial. Tuber globose, in flowering individuals 4--18 mm in diameter. Stem 16--40(--50) cm, usually slightly curved, glabrous or pubescent in the lower part. Underground part of stem flexuose, up to 10 cm long. Number of branches 0--4, the lowest usually originating from the upper half of stem, curved. Basal leaves triangular, 3-pinnate, lobes narrowly lanceolate, acute; upper cauline leaves 1--(--2)-pinnate, lobes linear to filiform, 0.3--1.1 mm broad, usually not more than 0.5 mm; cauline leaves glabrous, without short unicellular hairs; leaf sheaths ciliate or glabrous. Number of umbels 1--5; the terminal umbel with 4--9 rays; rays (7--)10--35(--45) mm long. Bracts lacking. Bractlets (2--)5(--6), triangular to narrowly lanceolate, up to 3 mm long, glabrous, without membraneous margin. Petals white, 1.5 times as long as broad. Anthers pink. Stylopodium green at anthesis. Pedicels without small teeth at apex. Fruit black linear-oblong, 3.8--5.8 mm long; ridges prominent; vittae one per interval; style and stylopodium 1.2--2.2 mm long; styles erect or slightly divergent; stylopodium forming a distinct collar at maturity. Chromosome number 2n=20. Illustration Fig. 6.

Flowering period: April, May.

Fig. 6. Geocaryum stylosum. -- A: Habit (Samos). -- B: Habit (Kemalpasa Dagh). -- C: Sideview of stylopodium at anthesis. -- D: Apex of pedicel with part of carpophore. -- E: Mericarp. -- F: Transverse section of mericarp. -- G: Bractlets. -- A, B: X0.5. -- C, D: X20. -- E, G: X8. -- F: X40.

Distribution and habitat: G. stylosum is distributed in W and SW Turkey and on the island of Samos. It grows in Pinus brutia forest in mountains from 600 to 1150 m. Other species found associated with G. stylosum on Kemalpaŝa Daĝh (E66) are: Asplenium obovatum, Briza spicata, Cheiranthus fragans, Luzula forsteri, Microsciadum minutum, Pinus brutia, Poa bulbosa f. vivipara, Salvia grandiflora, Trifolium speciosum, Vicia lathyroides. Species found on Samos (E67) are: Anthoxantum odoratum, Asplenium adiantum-nigrum, Campanula lyrata, Clinopodium vulgare ssp. orientale, Doronicum caucasicum, Lathyrus laxiflora, Pinus brutia, Pteridium aquilinum, Salvia grandiflora. (Fig. 8).

Variation and distinguishing characters: G. stylosum is a fairly uniform species although some variation is found between the different populations especially in size of fruit and in length of style and stylopodium. The leaves are always glabrous except the basal ones in the collection from Mugla which has unicellular hairs not more than 0.3 mm long.

G. stylosum belongs to the Aegean species group which is recognized by the collar-shaped stylopodium and lack of teeth at the apex of the pedicels. It is distinguished from G. bornmuelleri and G. macrocarpum by the very slender habit and the filiform lobes of the cauline leaves. It is usually only branched in the upper part of the stem. G. stylosum is somewhat similar to G. capillifolium but is distinguished by the lack of teeth at the apex of pedicels and the lack of unicellular hairs on lobes of cauline leaves. The stylopodium is green at anthesis and the anthers are pink.

GEOCARYUM BORNMUELLERI (WOLLF) ENGSTRAND COMB. NOV.

Biasolletia Bornmülleri Wollf 1921. Feddes Repert. 17, p. 43. -- Freyera Bornmülleri (Wollf) Hayek 1927 p. 995. -- Orig. coll.: Sintenis and Bornmüller. It. turcic. n. 654. Insel Thasos (1891). (lectotype in G, isotype in

G, LD, S, W, WU, WU (Herb. Halácsy)).

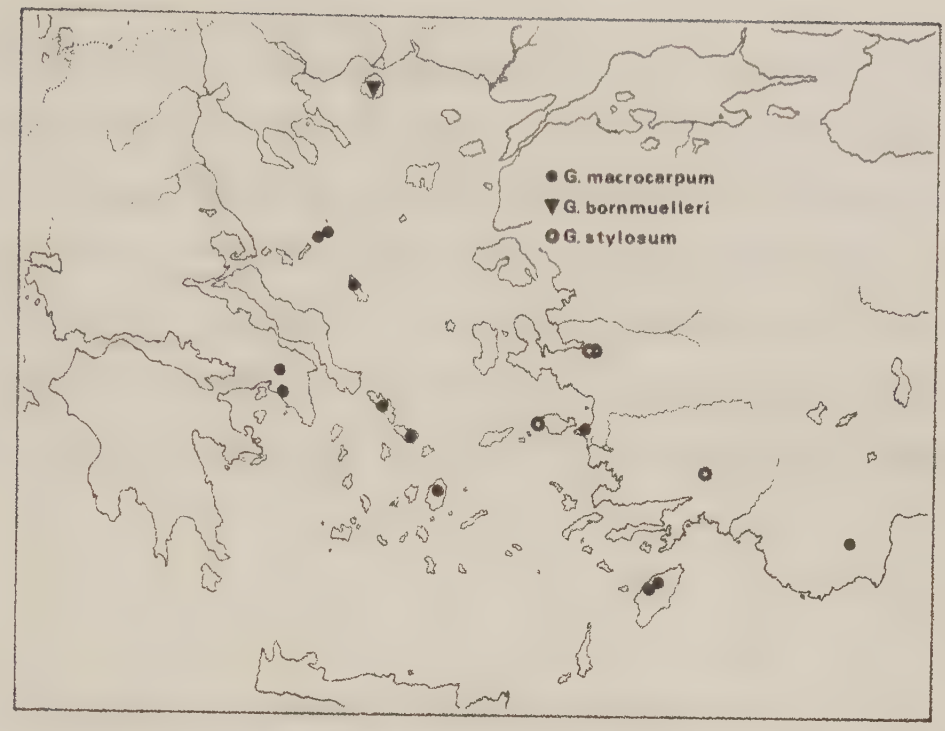
Description: Erect, stout perennial. Tuber globose, in flowering individuals up to 19 mm in diameter. Stem 30--75 cm, striate, glabrous, sometimes shortly pubescent in the lowest part. Underground part of stem short, 1--5(--9) cm. Number of primary branches usually 3--4, usually with secondary branches; uppermost branches always exceeding the terminal umbel. Basal leaves broadly triangular in outline, 3--4-pinnate, ultimate lobes 5--15 mm long, narrowly lanceolate, acute; upper cauline leaves rather similar to the basal ones but reduced, 2--3-pinnate, leaf lobes linear, usually 11--15 mm long, rarely up to 35 mm, petiole short, sometimes only consisting of a sheath; leaf sheaths ± ciliated at margins; leaf lobes sometimes with small unicellular teeth; petioles and rachis sometimes sparsely ciliate. Number of umbels varying from 1 to at least 12; terminal umbel with 11--25 rays; rays 28--55 mm long, homogeneously curved. Bracts present in most individuals, usually 1 or 2, but sometimes up to 5, of shape as bractlets. Bractlets (3--)4--6, narrowly ovate up to 6 mm long with 3 or more parallel veins, usually with a white margin. Petals white. Anthers greenish-white. Stylopodium green at anthesis. Pedicels without teeth at apex. Fruit black, linear-oblong, 5--6 mm long; ridges prominent; styles in fruit slightly divergent; length of style and stylopodium 1.2--1.7 mm. Chromosome number not known. Illustration Fig. 7.

Flowering period: End of April to beginning of June.

Distribution and habitat: G. bornmuelleri is only known from the original collection by Sintenis and Bornmüller. The island of Thasos is situated in the northern Aegean Sea, SE of the city of Kavalla. The collector's description of the locality is "Theologos, in fruticetis". Such areas around the village of Theologos have been investigated twice by the author but without result. (Fig. 8).

Variation and distinguishing characters: G. bornmuelleri belongs to the

Fig. 7. Geocaryum bornmuelleri. -- A: Upper and lower part of stem. -- B: Fruit. -- C: Apex of pedicel with part of carpophore. -- D: Bractlets. -- A: X0.5. -- B, D: X8. -- C: X20.



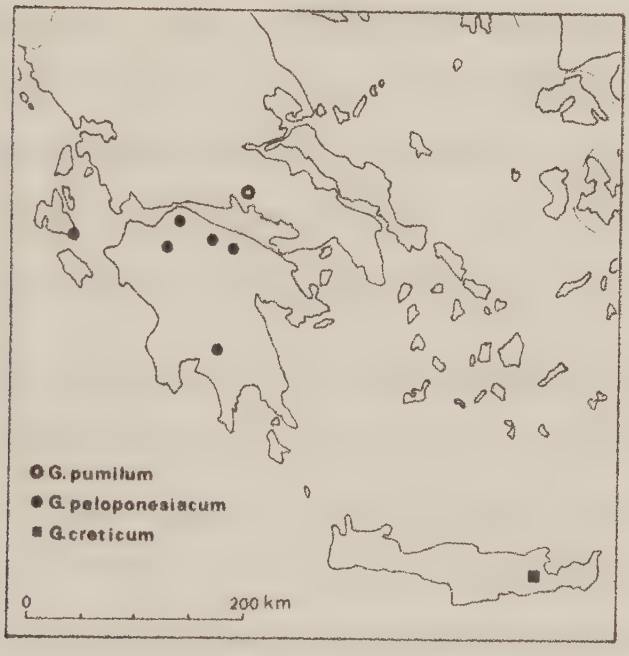


Fig. 8. Distribution of examined material. -- Above: G. macrocarpum, G. bornmuelleri and G. stylosum. -- Below: G. pumilum, G. peloponesiacum and G. creticum.

Aegean group of species. Thus the stylopodium forms the typical collar at maturity and the pedicels are not toothed. It is easily distinguished from G. macrocarpum and G. stylosum by the stout habit and the large number of rays in the terminal umbel. In the erect habit and lanceolate bractlets G. bornmuelleri somewhat resembles G. tuberosum. It is, however, distinguished by the large number of rays in the terminal umbel and by the lack of teeth on the pedicels. It can also be distinguished from G. capillifolium on the same characters.

GEOCARYUM PUMILUM (SIBTHORP & SMITH) NYMAN

Nyman 1854--1855 p. 166. -- Bunium pumilum Sibthorp & Smith 1806. Fl. Graec. Prodr. p. 187. -- Huetia pumila (Sibth. & Smith) Boissier & Reuter 1856 p. 103. -- Freyera pumila (Sibth. & Smith) Boissier 1872 p. 897. -- Biasolettia pumila (Sibth. & Smith) Nyman 1879 p. 302. -- Orig. coll.: Sibthorp, In monte Parnasso (lectotype: Flora graeca t. 274).

Comments: The combination Geocaryum pumilum made by Nyman is without comments and with a question mark. It has not been possible to trace any sheet of G. pumilum which could possibly have been seen by Sibthorp and Smith at the time of publication. The picture in Icon. Fl. Graeca is excellent and very typical of the species. It is presented as Bunium alpinum Waldst. & Kit.

Description: Procumbent perennial. Tuber usually regularly globose, in flowering individuals (4--)9--13(--15) mm in diameter. Plant 3--17 cm high. Underground part of stem long and flexuose. Number of primary branches 0--4, usually 1 or 2, often exceeding the terminal umbel; branches often forming an obtuse angle with the main stem. Basal leaves broadly triangular in outline, basal segments long-petiolate, up to 2.5 cm, ultimate lobes lanceolate, sub-obtuse, petiole up to 12 cm; cauline leaves strongly reduced, often only

consisting of a sheath. Number of umbels 1--5, usually 2 or 3; terminal umbel with 1--4 rays, usually 3; rays (6--)14--20(--35) mm long, slightly curved; peduncle of terminal umbel short, (0--)1--9(--31) mm, glabrous or tomentose. Bracts lacking. Bractlets 1--4, usually 2 or 3, 2.0--5.7 mm long and c. 1 mm broad, lanceolate to oblong with more or less crispate hairs on the margin, sometimes also on the surface. Petals white. Anthers dark red. Stylopodium white at anthesis. Apex of pedicels without teeth. Fruit black, lanceolate--oblong, (3.9--)4.3--5.3(--6.2) mm long; ridges prominent, usually with small teeth, especially on upper part of fruit; styles and stylopodium c. 1 mm long; styles slightly divergent; vittae one per interval, commissural ones usually missing. Chromosome number 2n=20. Illustration Fig. 9.

Flowering period: June to August.

Distribution and habitat: G. pumilum is endemic to Parnassos in S Greece. It grows in the alpine parts of the mountain, in stony and open areas from 1800 to 2400 m. Other species found in the same locality as collection E26 are: Campanula radicosa, Carduus armatus, Daphne oleoides, Myosotis olympica, Phleum commutatum, Poa trichopoda. (Fig. 8).

Variation and distinguishing characters: The dentition of the fruits varies. The presence of teeth is correlated to presence of hairs on the peduncle (see VI Morphological variation).

G. pumilum belongs to the same group as G. creticum and G. peloponesiacum. This group is distinguished from all other species by the dark red anthers. G. pumilum is distinguished from G. peloponesiacum by the pubescent bractlets and from G. creticum by the only slightly divergent styles.

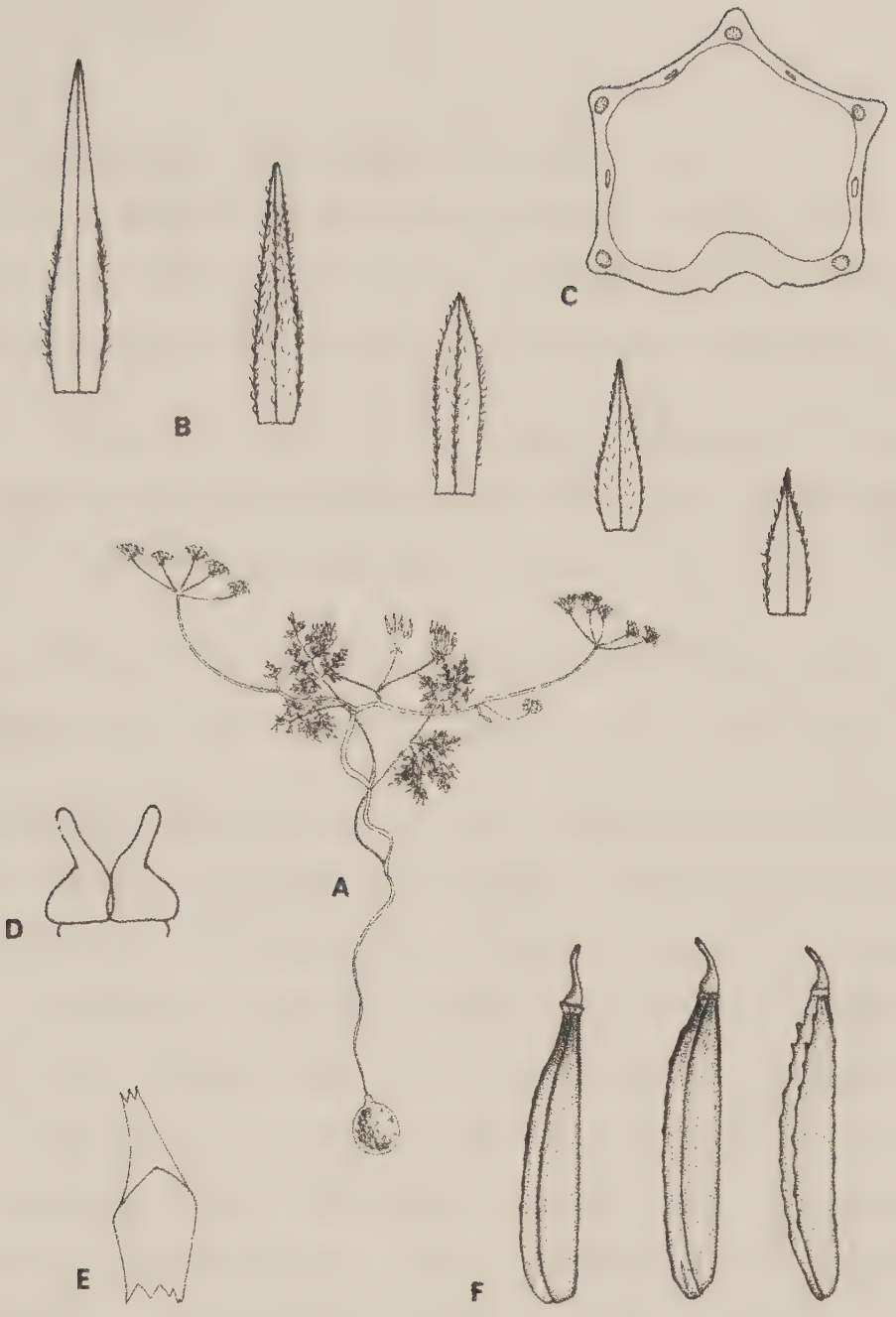


Fig. 9. Geocaryum pumilum. -- A: Habit. -- B: Bractlets. -- C: Transverse section of mericarp. -- D: Sideview of stylopodium at anthesis. -- E: Apex of pedicel with part of carpophore. -- F: Mericarps. -- A: X0.5. -- B, F: X8. -- C: X40. -- D, E: X20.

GEOCARYUM PELOPONESIACUM ENGSTRAND SPEC. NOV.

Species Geocaryi antheris atropurpureis distincta. Geocaryo pumilo similis, sed differt involucello glabro, radiis umbelli terminalis brevioribus, pedunculis longioribus. A Geocaryo cretico stylis erectis dignoscitur.

Orig. coll.: Halácsy Iter Gr. sec.: Gr. Achaia. In rupestribus calcareis regiones superioris mt. Panachaicon (Vodia hodie) supra urbem Patras. Alt. 1500--1800 m. 5.6.1893. (holotype in G, isotype in K, LD, LY, UPS, W, WU).

Comments: This species has been considered by different authors to be part of G. parnassicum, G. macrocarpum, G. pumilum and G. divaricatum.

Description: Procumbent perennial. Tuber irregularly globose, (4--)11--17 (--20) mm in diameter in flowering individuals. Plant (2--)4--22(--30) cm high. Underground part of stem long and flexuose. Number of branches 1--5, usually 2--3, often with secondary branches; most branches exceeding the terminal umbel. Basal leaves broadly triangular, 3-pinnate, ultimate lobes lanceolate-elliptic, acute or subobtuse, petiole up to 10 cm; cauline leaves gradually becoming reduced from the base upwards, lobes like those of the basal leaves or somewhat elongate. Number of umbels varying, usually 2--4 but sometimes up to more than 15; terminal umbel with 2--6 rays; length of rays (3--)6--14(--26) mm; length of peduncle (0--)15--30(--66) mm. Bracts lacking. Bractlets 1--5, usually 2--4, narrow triangular or lanceolate, 1.0--4.0 mm long; margin usually glabrous, rarely ciliate with short hairs. Stylopodium white at anthesis. Apex of pedicels without teeth or rarely with very small ones. Fruit black, linear-oblong, gradually tapering at apex making the fruit shortly beaked, 4.0--6.0 mm long, c. 2 mm broad; ridges more or less prominent, filiform; styles short, erect or slightly curved; vittae lacking or 4 interjugale ones; commissural vittae lacking. Chromosome number 2n=20. Illustration Figs. 10, 11.

Fig. 10. Geocaryum peloponesiacum. -- A: Habit. -- B: Branch. -- C: Apex of pedicel with part of carpophore. -- D: Bractlets. -- E: Sideview of stylopodium at anthesis (Mt Killini). -- F: Sideview of stylopodium at anthesis (Kefallinia). -- G: Mericarps. -- H: Transverse sections of mericarps. -- A, B: X0.5. -- C, E, F: X20. -- D, G: X8. -- H: X40.

Fig. 11. Geocaryum peloponesiacum. Different modificative forms from Mt Panakhaikon. X0.5.

Flowering period: May to July.

Distribution and habitat: G. peloponesiacum grows in the mountains of Peloponnisos and on the island of Kefallinia. It is mostly found in open and stony places, often on screes, from 1400 to 2000 m. On Kefallinia it grows in an open Abies cephallonica forest. The water supply comes mainly from melting snow. Near the top of Mt Killini it is found flowering just at the edge of the melting snow. Associated species found on Keffalinia (E14) were: Abies cephallonica, Astragalus sempervirens ssp. cephalonicus, Crepis fuliginosa, Leontodon graecus, Petrorhagia saxifraga, Scuttelaria rubicunda ssp. cephallonica. On Mt Killini (E17): Astragalus angustifolius ssp. angustifolius, Carum rigidum, Cerastium illyricus, Dianthus serratifolius, Erodium chrysanthum, Linum punctatum, Poa bulbosa, Scilla bifolia, Viola chelmaea, Viola gracilis. On Mt Panakhaikon (E12): Astragalus parnassi ssp. cylleneus, Eryngium campestre, Festuca ovina, Lactuca viminea, Melica ciliata, Scandix australis, Stipa pennata. (Fig. 8).

Variation and distinguishing characters: G. peloponesiacum is closely related to G. pumilum and G. creticum. The distinguishing characters are given under those species. Unlike G. pumilum and G. creticum this species has a rather wide range of variation especially as regards height of plant, number of rays, number of branches. Part of variation is due to modification as found on Mt Panakhaikon (see Fig. 11). There is also a strong regional differentiation.

Dubious specimens: From the surroundings of Patras (Peloponnisos) there are two collections which are difficult to classify. One was made by Halácsy 1893 from "Achaia. In collibus lapidosis prope urbem Patras. Alt. 30 m. Solo calcareo. Legi d. 4 Junii." The other was made by Heldreich 1899 in "Achaia: in m. Omplo pr. Patras. 5 Junii." Altogether there are 8 individuals. It is an erect, rather stout plant, 27--48 cm high, branches 2 or lacking. The

number of rays in the terminal umbel is 9--14 and the length of the rays is 18--51 mm. The pedicels are without teeth at the apex. The fruits are not quite ripe but the length is estimated to be from 4 to 5 mm. The collar around the dry style is conspicuous. There are 4--6 narrowly lanceolate bractlets. The leaf lobes are almost linear. As there are no flowers it is impossible to state the colour of the anthers.

It has been shown above that G. peloponesiacum shows great altitudinal modification. This may be an extreme lowland form of this species. However, the non-toothed pedicels and the conspicuous collar indicate a close connection with the Aegean species. Until further information is available, especially on the colour of the anthers and the colour of the fresh stylopodium, these plants will be regarded as a deviating form of G. peloponesiacum.

GEOCARYUM CRETICUM (BOISS. & HELDR.) ENGSTRAND COMB. NOV.

Butinia Cretica Boissier & Heldreich 1849. Diagn. Pl. Or. Nov. 2(10), p. 50. -- Freyera Cretica (Boiss. & Heldr.) Boissier & Heldreich 1856 p. 101. -- Biasolettia cretica (Boiss. & Heldr.) Nyman 1879 p. 303. -- Huetia cretica (Boiss. & Heldr.) P.W. Ball 1968 p. 16. -- Orig. coll.: Heldreich 1846. Creta, in lapidosis montium Lassiti ad nives. (lectotype in G (Herb. Boiss.), isotypes in G (Herb. de Candolle), W, WU (Herb. Halácsy)).

Comments: Hammatocaulis cretica Tausch 1834 is sometimes cited as a synonym of Freyera cretica (e.g. Rechinger 1943). This name is, however, a synonym of Ferula nodosa (L.) Boiss. G. creticum should not be confused with Bunium creticum Miller (Bunium creticum D'Urville). The correct name of this species is Scaligeria napiformis (Sprengel) Grande (cf. Greuter & Rechinger 1967 and Engstrand 1970).

Description: Procumbent perennial, tuber more or less globose, in flowering individuals 8--18 mm in diameter. Plant 3--12 cm high. Underground part of stem long and flexuose. Number of branches 1--5, usually 1 or 2; branches generally at an obtuse angle to the stem. Basal leaves broadly triangular, 2--3-pinnate, basal segments long petiolate, 1.0--1.5 cm, ultimate lobes elliptical, 3--6 mm long, c. 2 mm broad, subobtuse, petiole up to 10 cm; lobes of cauline leaves similar to those of the basal ones; upper cauline leaves strongly reduced, usually 1-pinnate, petiole consisting of a sheath. Number of umbels 1--7, usually 2--4; terminal umbel with 1--3 rays; rays 0.5--22.0 mm long; length of peduncle varying from 3.5 to 45.0 mm. Bracts lacking. Bractlets 2--3, very variable in shape, ovate to lanceolate to triangular, up to 2.5 mm long, c. 1 mm broad, sometimes with scarious margin, margins ciliate or glabrous. Petals white. All flowers almost actinomorphic. Anthers dark red. Stylopodium white at anthesis. Apex of pedicels without teeth. Fruit black, linear-lanceolate, gradually tapering at the apex making the fruits shortly beaked, 5.0--6.0 mm long, ridges prominent, styles and stylopodium more than 1.5 mm long, styles strongly backward curving; vittae lacking at maturity. Chromosome number 2n= 20. Illustration Fig. 12.

Flowering period: May to July.

Distribution and habitat: G. creticum is endemic to Crete where it is found on the mountain Dhikti Oros (Aphendi Christos) in Lasithi. (According to Halăcsy 1901 it was also found on Idhi Oros by Heldreich). It grows on stony slopes and screes from 1300 to 1700 m. The vegetation in this area mainly consists of dwarf shrubs which are often spiny. Associated species found in the locality for collection E20 are Astragalus creticus ssp. creticus. Berberis cretica, Centaurea idaea, Euphorbia acanthothamnos, Lactuca alpestris, Prunus prostrata. (Fig. 8).

Variation and distinguishing characters: G. creticum is said by previous

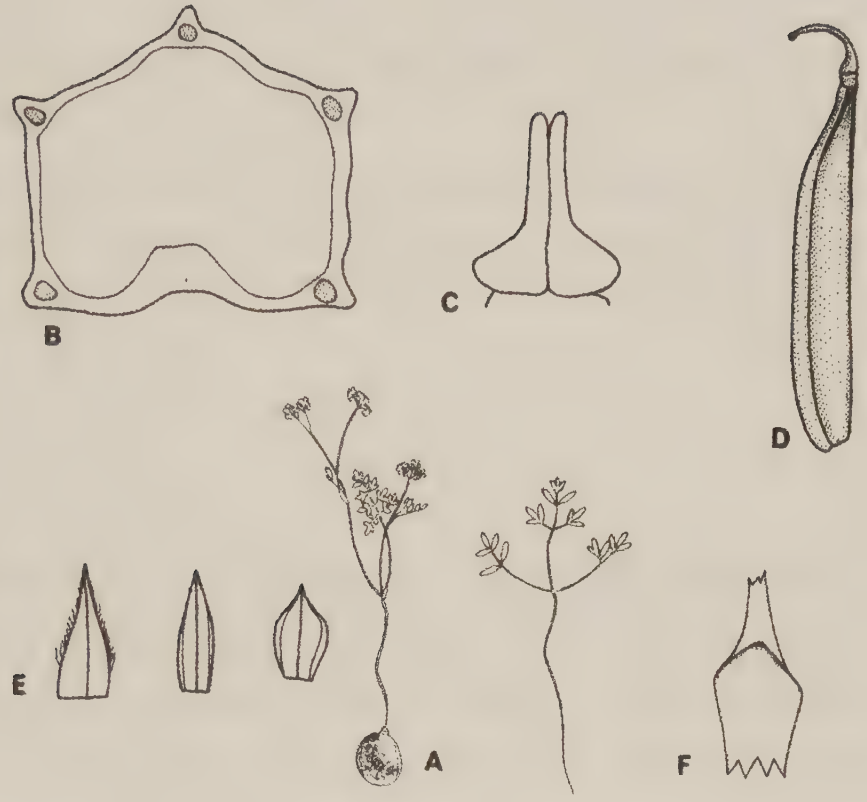
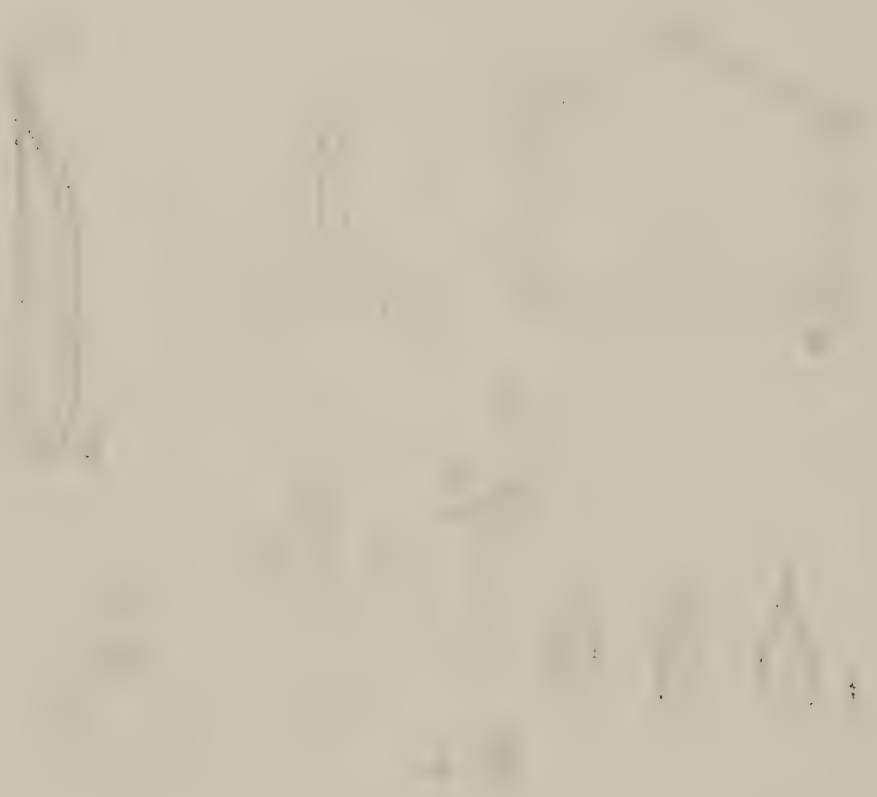


Fig. 12. Geocaryum creticum. -- A: Habit and basal leaf. -- B: Transverse section of mericarp. -- C: Sideview of stylopodium at anthesis. -- D: Mericarp. -- E: Bractlets. -- F: Apex of pedicel with part of carpophore. -- A: X0.5. -- B: X40. -- C, F: X20. -- D, E: X8.



authors to be distinguished from all other species of Geocaryum on the ciliate bractlets. This is not so. The bractlets of G. creticum are sometimes glabrous and those of G. peloponesiacum, G. pumilum and G. pindicola are sometimes shortly ciliate. Modificative changes due to altitudinal differences seem to be very small or lacking.

G. creticum belongs the pumila-complex recognized by the dark red anthers. It is distinguished from all other species by the styles which are homogeneously backwards curved.

GEOCARYUM PINDICOLA (HAUSSKN.) ENGSTRAND COMB. NOV.

Biasolettia pindicola Haussknecht 1893. Mitt. Thür. Bot. Ver. Nov. ser. V, p. 114. -- Freyera parnassica Boiss. & Heldr. B. pindicola (Hausskn.) Hayek 1927 p. 994. -- Orig. coll.: Haussknecht 1885. Hab. in saxosis P.D. ad Gion Skala supra Sermeniko (holotype in Jena (Herb. Hausskn.)), (two isotypes in Jena).

Biasolettia pindicola var. alpina Freyn & Sintenis 1897 p. 613. -- Orig. coll.: Sintenis 1895 (Exsicc. 651): Thessalia graeca: Pindus tymphaeus: in cacumine montis Peristeri. 2 Julio. (lectotype in Jena (Herb. Hausskn.), isotype in LD, WU, WU (Herb. Halácsy)).

Comments: The name B. pindicola first appeared in Nyman 1889. He wrote "B. pindicola Hsskn. ms. (litt. 1889)" and cited the locality. It is obvious that the name was mentioned by Nyman in anticipation of a future valid publication. Therefore the correct year of publication is 1893.

Description: Procumbent, rarely erect perennial. Tuber usually irregularly globose, very variable in size, from 4--40 mm in diameter, usually 10--20 mm. Plant 7--35 cm high. Underground part of stem long and flexuose. Number of

primary branches 0--4, usually 1 or 2, generally exceeding the terminal umbel, often with secondary branches. Basal leaves broadly triangular in outline, ultimate lobes lanceolate to oblong, acute, 3--13 mm long, petioles long, flexuose; cauline leaves reduced, uppermost ones more often pinnate, rarely only consisting of a sheath. Umbels 1--5 or more; terminal umbel with (2--) 4--6(--7) rays; rays 5--39 mm long; peduncle length variable. Bracts lacking. Bractlets 1--5, usually 2--4, lanceolate or narrowly triangular, glabrous or rarely shortly ciliate, usually green with reddish midvein and margins. Sepals minute. Petals white or reddish. Anthers white or greenish or rarely pink. Stylopodium white at anthesis. Apex of pedicels sometimes with small teeth. Fruit black, lanceolate-oblong, 3.8--6.6 mm long; ridges prominent; styles and stylopodium 0.9--1.7 mm long; styles slightly divergent; vittae generally missing at maturity, rarely one per interval. Chromosome number 2n=20. Illustration Fig. 13.

Flowering period: June, July.

Distribution and habitat: G. pindicola grows in the mountains from S Albany to Mt Parnassos in Greece, its main distribution being the Pindos Mts. It grows mainly in the alpine regions from 1600 to 2300 m. The plant is found on stony slopes and screes, sometimes on grassy ground. Other associated plants found on Mt Oité (E24) are: Cerastium candidissimum, Daphne oleoides, Festuca ovina, Sanguisorba minor, Trisetum flavescens. (Fig. 14).

Variation and distinguishing characters: G. pindicola is a very variable species but fairly homogeneous within each population. For instance populations from Albany are recognized by the long, more or less erect branches well exceeding the terminal umbel. Plants from Mt Peristeri are procumbent and similar in habit to G. pumilum. Plants from Mt Kazarma are about 30 cm high, much branched and with long rays. G. pindicola most closely resembles the species

Fig. 13. Geocaryum pindicola. -- A: Plant from Mt Giona. -- B: Plant from Mt Kauki. -- C: Plant from Mt Peristeri. -- D: Mericarps from Mt Oiti (to the left) and Mt Timfristos. -- E: Bractlets. -- F: Transverse section of mericarp from Mt Timfristos. -- G: Transverse section of mericarp from Mt Oiti. -- H: Apex of pedicel with part of carpophore. -- I: Side-view of stylopodium at anthesis. -- A, B, C: X0.5. -- D, E: X8. -- F, G: X40. -- H, I: X20.

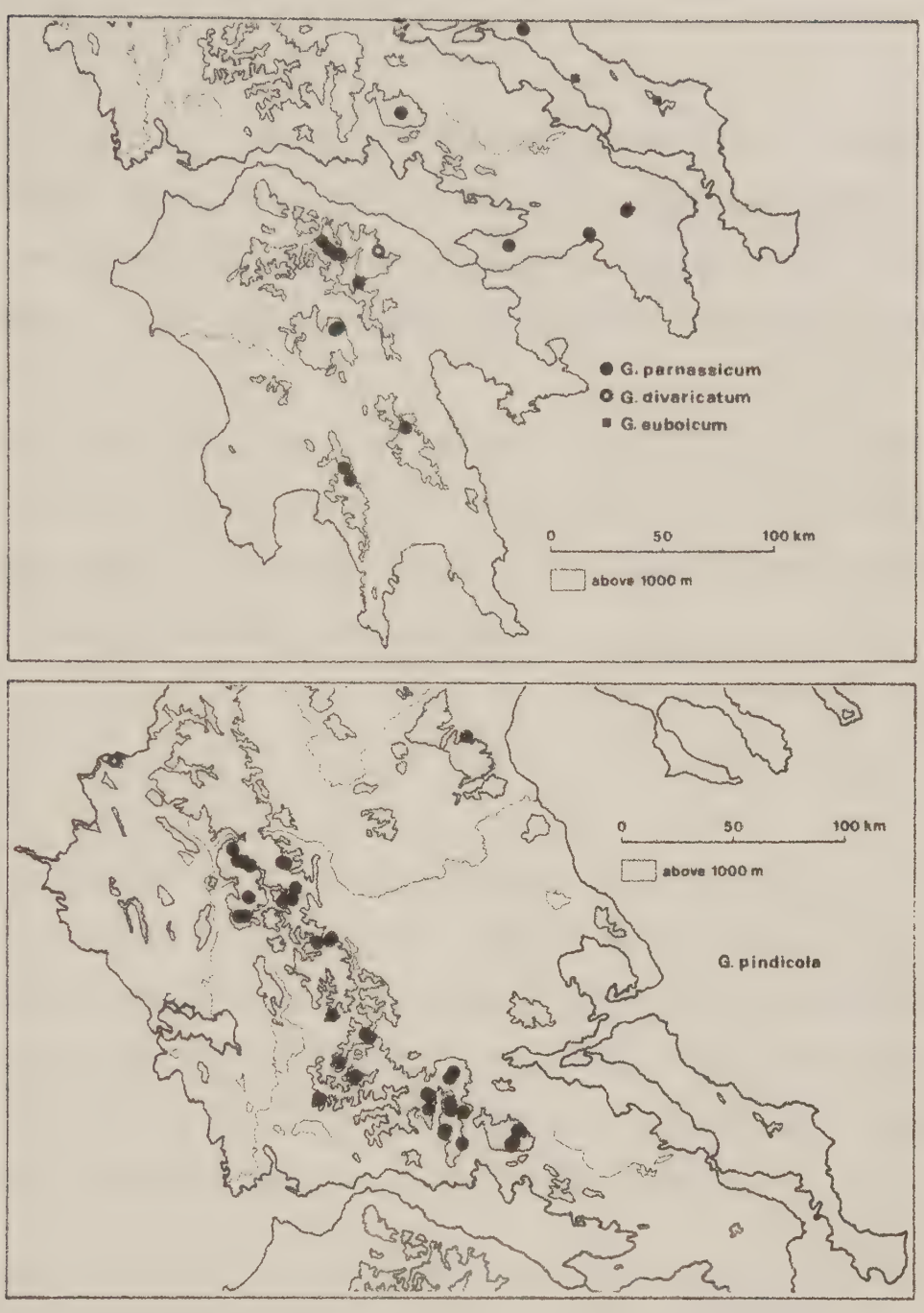


Fig. 14. Distribution of examined material. -- Above: G. parnassicum, G. divaricatum and G. euboicum. -- Below: G. pindicola. The star indicate a locality which is inexactly known, it represents a mountain range.

in the pumilum-complex but is distinguished by the white to greenish anthers. It is distinguished from G. macrocarpum by the stylopodium which is more or less attenuate into the styles not forming the typical collar. G. parnassicum is slenderer and has smaller fruits. The uppermost leaves of G. parnassicum are generally undivided.

Material newly collected on Mt Olympos, Greece (Strid & Kjellson 11326) differs in being very slender and c. 40 cm high. It has longer rays and pink or reddish anthers. It is here regarded as an extreme variant of G. pindicola but is in need of further investigation.

GEOCARYUM CYNAPIOIDES (GUSS.) ENGSTRAND COMB. NOV.

Myrrhis cynapioides Gussone 1826 (a). Plantae rariores etc., p. 127. -- Bunium cynapioides (Guss.) Bertoloni 1837(1838) p. 217. -- Freyera cynapioides (Guss.) Grisebach 1845 p. 366. -- Biasolettia cynapioides (Guss.) Drude 1898 p. 150. -- Huetia cynapioides (Guss.) P.W. Ball 1968 p. 16. -- Orig. coll.: Gussone. Valle d'Orfenta alla Majella (holotype in NAP (Herb. Gussone)).

Comments: It has not been possible to have the original material in Napoli on loan but the identity of the sheet has been checked. Gussone has presented an illustration in Plantae rariores, icones tab 24 (1826 b). It is somewhat diagrammatic, especially as regards the shape of the tuber and the fruit but the identification is clear.

Description: Erect perennial. Tuber globose, in flowering individuals 4--18 mm in diameter. Stem (20--)25--40(--52) cm, distinctly striate, generally pubescent in the lower part. Underground part of stem short, 1--2 cm. Number of branches 0--3, usually exceeding the terminal umbel. Basal leaves triangular in

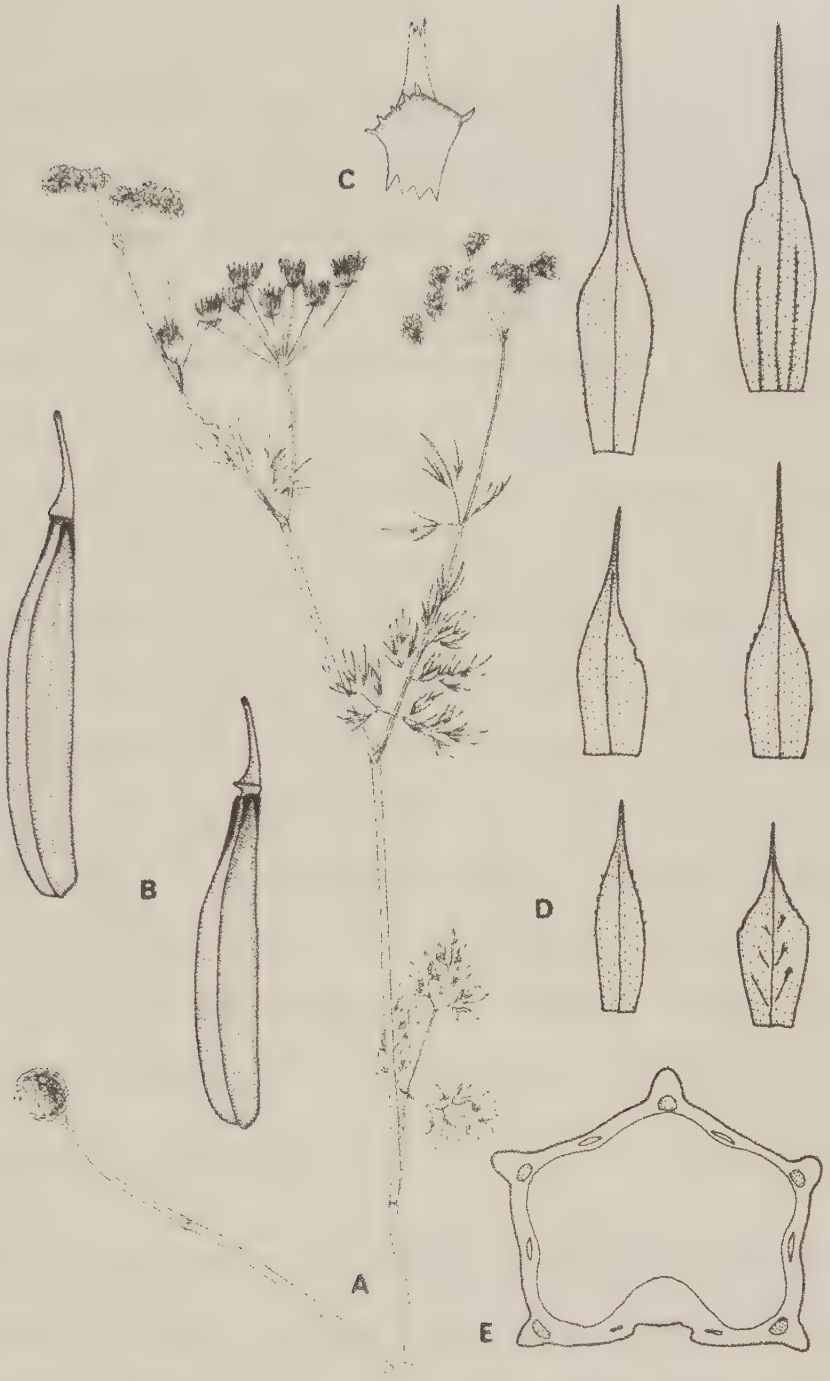


Fig. 15. Geocaryum cynapioides. -- A: Habit. -- B: Mericarps. -- C: Apex of pedicel with part of carpophore. -- D: Bractlets. -- E: Transverse section of mericarp. -- A: X0.5. -- B, D: X8. -- C: X20. -- E: X40.

outline, 3-pinnate, ultimate lobes lanceolate, 3--7 mm long, petioles up to 15 cm long, usually shorter; upper cauline leaves broadly triangular in outline, 1--3-pinnate, very rarely undivided, lobes narrowly lanceolate to linear, up to 25 mm long, usually more than 1 mm broad; leaf sheaths ciliate; leaf lobes always with distinct unicellular teeth, usually in several rows at margin and one line below on the distinct midvein. Number of umbels 1--4; terminal umbel with (5--)7--10(--13) rays; rays (8--)15--30(--33) mm long, fairly straight making the umbel broom-like. Bracts lacking. Bractlets (4--)6--7(--8), 2.5--10.0 mm long usually 1--2 mm broad with a basal lanceolate part but often with a setose point, up to 6 mm long, margin glabrous or shortly ciliate, midvein sometimes branched, rarely with two lateral veins. Petals white. Anthers greenish-white. Stylopodium green at anthesis. Pedicels with teeth at apex. Fruit black to brownish, linear-oblong, gradually narrowed at apex, 5.0--6.5 mm long; ridges prominent; styles in fruit slightly divergent; length of style and stylopodium 1.2--1.8 mm; vittae one per interval, usually two on the commisural side. Chromosome number 2n=18. Illustration Fig. 15.

Flowering period: July, August.

Distribution and habitat: G. cynapioides has a very delimited distribution in some mountains in Abruzzi in Italy. It is known from several collections from above 1200 m. The species is found on dry stony slopes and in pastures, sometimes in the shade of thickets of Fagus. Other associated species found on Mt Morrone (E44) are: Cynoglossum magellensis, Dactylis glomerata, Echium vulgare, Epilobium montanum, Fagus sylvatica, Lamium garganicum, Pteridium aquilinum, Veronica chamaedrys. (Fig. 17).

Variation and distinguishing characters: The species is uniform. The only variation of importance is found in the bractlets which are not setaceous in some individuals.

G. cynapioides most closely resembles G. tuberosum but is distinguished on the brownish fruits, the numerous teeth of the cauline leaf lobes and by the basal leaves where the lobes not are distinctly crowded in the three corners of the leaf. In this last character G. cynapioides more closely resembles G. capillifolium.

GEOCARYUM TUBEROSUM (KOCH) ENGSTRAND COMB. NOV.

Biasolettia tuberosa Koch 1836. Flora oder allgem. bot. Zeitung (Regensb.), p. 163. -- Freyera tuberosa (Koch) Reichenbach H. G. 1866 p. 92. -- Bunium cynapioides (Guss.) Bertoloni β Tuberosum (Koch) Paoletti 1900 p. 157. -- Orig. coll.: "auf dem Monte maggiore in Istrien und auf dem Velebit bei Pago in Dalmatia", collected by Biasoletto (lectotype in L).

Chaerophyllum Biasoletti Beck von Mannagetta 1895 p. 212. -- Nom. superfl.

Comments: The publication of B. tuberosa is referred to as Koch 1837. Syn. Fl. Germ. but the first publication was in Flora (Regensb.) in a paper entitled "Biasolettia und Hladnikia, zwei neue Gattungen der Doldengewächse". The description was based on four sheets which Koch received from Biasolletto. Two were collected on Mt Maggiore and two on Mt Velebith. The sheet in Leiden, which is suggested as lectotype, was collected in "Velebit prope Pago" and has been seen by Koch. Chaerophyllum Biasoletti Beck von Mannagetta is based on Biasolettia tuberosa Koch.

Description: Erect perennial. Tuber globose, in flowering individuals 8--25 mm in diameter. Stem (18--)30--60(--84) cm, striate, glabrous or oftener with hairs up to 2 mm long on the basal part. Underground part of stem short, 1--4 cm. Number of branches 0--2(--3). Basal leaves broadly triangular in outline, 2--3-pinnate, ultimate lobes 3--8 mm long, lanceolate, lobes crowded at the

Fig. 16. Geocaryum tuberosum. -- A: Habit. -- B: Mericarps. -- C: Bractlets. -- D: Sideview of stylopodia at anthesis. -- E: Apex of pedicel with part of carpophore. -- F: Transverse section of mericarp. -- A: X0.5. -- B, C: X8. -- D, E: X20. -- F: X40.

three corners of the leaf, petiole up to 15 cm long, usually shorter; upper cauline leaves broadly triangular in outline, usually 3-pinnate, lobes lanceolate to narrowly lanceolate rarely linear, (2--)4--10(--20) mm long, c. 1 mm broad; leaf sheaths usually ciliate; leaf lobes with small unicellular teeth at the margins. Number of umbels 1--3(--4); the terminal ones with (5--)7--10(--14) rays; rays (11--)20--40(--69) mm long, homogeneously curved. Bracts 0(--3). Bractlets (1--)4--7(--9), 2--5 mm long, up to 1,5 mm broad, lanceolate to ovate, sometimes with a very narrow whitish margin, rarely with lateral veins, midvein sometimes pinnately branched. Petals white. Most individuals with small teeth at apex of pedicels. Anthers greenish-white. Stylopodium greenish at anthesis, without a conspicuous border to the white styles. Fruit black, linear-oblong, gradually narrowed at top, 4.6--7.4 mm long, usually 5--6 mm; ridges prominent; styles in fruit only slightly divergent; length of style and stylopodium 1.0--1.9 mm; vittae one per interval, usually two on commissure. Chromosome number 2n=18(0--4)B. Illustration Fig. 16.

Flowering period: May to July.

Distribution and habitat: G. tuberosum is distributed on mountains along the eastern Adriatic coast, from Istria to N Albania. The altitudinal differences are considerable. The species is found from 600 m to 1800 m. It grows in stony open forests and scrub of mainly Fagus sylvatica and Quercus species. The following associated species were found in E52: Aristolochia rotunda, Clematis viticella, Filipendula vulgaris, Lathyrus latifolius, Myosotis silvatica, Orlaya grandiflora, Quercus pubescens. E53 was collected in a Fagus forest: Ajuga genevensis, Bromus erectus, Bunium alpinum ssp. montanum, Dactylis glomerata, Fagus sylvatica, Helianthemum nummularium, Neottia nidus-avis, Salvia pratensis, Sanguisorba minor, Sorbus aria, Rosa pendulina. (Fig. 17).

Variation and distinguishing characters: There is some variation in quantitative characters such as plant height and number of rays. In some plants

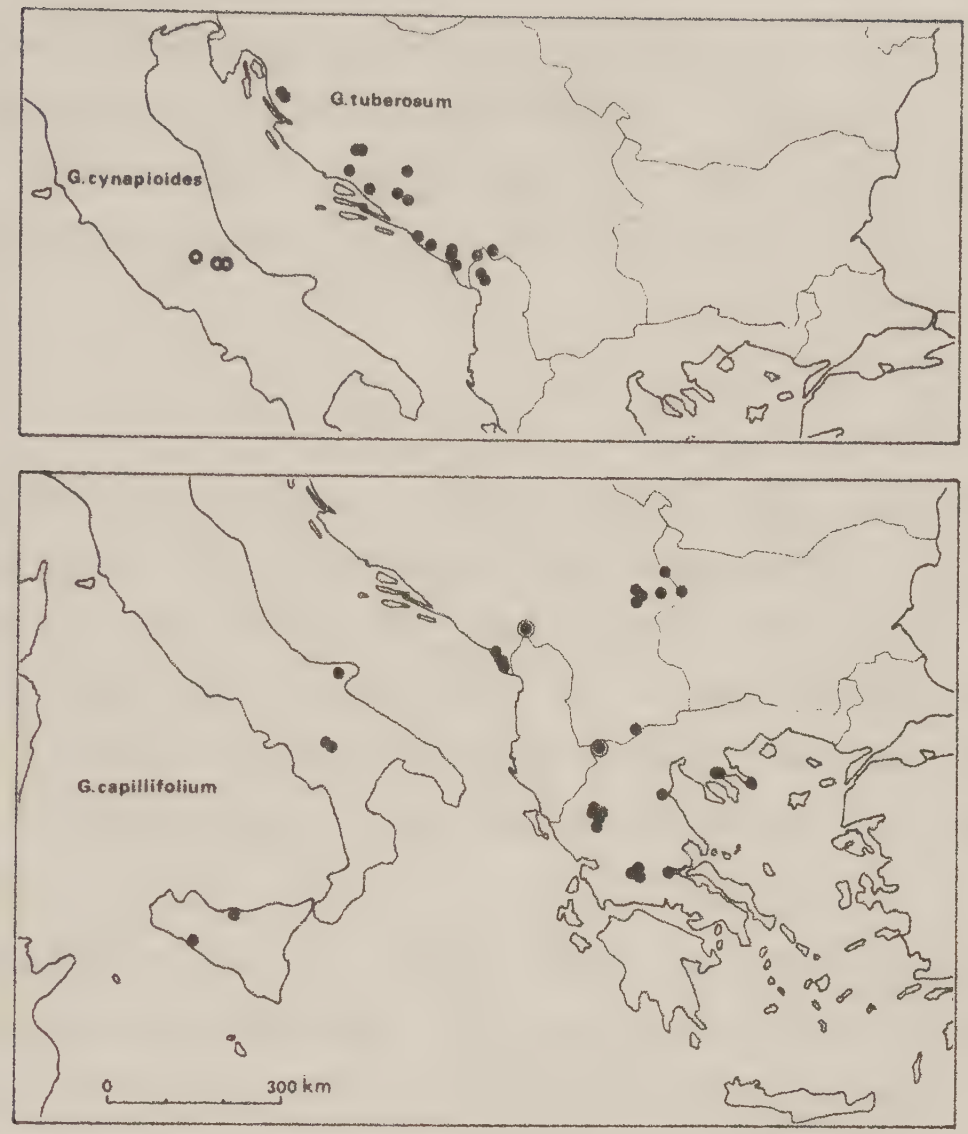


Fig. 17. Distribution of examined material. -- Above: G. cynapioides and G. tuberosum. -- Below: G. capillifolium. The rings indicate populations which are found to be tetraploid.

from Hercegovina, Nevesinje there are no teeth at apex of pedicels.

The differences between G. cynapioides and G. tuberosum are described under the first species. It is distinguished from G. capillifolium by the ± lanceolate leaf lobes, broader bractlets and larger fruits.

GEOCARYUM CAPILLIFOLIUM (GUSSONE) COSSON EMEND. ENGSTRAND

Cosson 1851 p. 113. -- Myrrhis capillifolia Gussone 1827. Fl. Sic. Prodr. I p. 351. -- Bunium capillifolium (Guss.) Bertoloni 1837 p. 219. -- Conopodium capillifolium (Guss.) Boissier 1845 p. 736. -- Bunium majus β capillifolium (Guss.) Fiori 1925 p. 42. -- Bulbocastanum capillifolium Todaro 1887 p. 261. -- Orig. coll.: Gussone. Sicilae meridionalis (lectotype in NAP (Herb. Gussone)).

Freyera congesta Boissier & Heldreich 1859 p. 88. -- Biasolettia congesta (Boiss. & Heldr.) Nyman 1865 p. 28. -- Orig. coll.: Samaritani & Guicciardi 1857. In cacumine jugi Petra m. Veluchi. 6000', 6 Aug. (holotype in G (Herb. Boissier), isotype in WU (Herb. Halácsy)):

Biasolettia balcanica Velenovský 1891 p. 399. -- Freyera Balcanica (Vel.) Halácsy 1892 p. 370. -- Biasolettia cynapioides C. balcanica (Vel.) Hayek 1927 p. 994. -- Orig. coll.: Vandas 1887. In herbis alpinis et subalpinis solo calcareo m. Balkan (Stara Planina) supra Bucina versus Sofiam. Specimen not found. -- Neotype: Adamovic 1892. In herbis montis Basara prope Pirot. WU:

Conopodium (?) graecum Freyn & Sintenis 1897 p. 612. -- Orig. coll.: Sintenis 1896 (exs. 648). Thessalia graeca. Pindus tymphaeus: in subalpinis montis Plaka prope Chaliki. 4 Julio (lectotype in G (Herb. Boiss.), isotypes in LD, W, WU, WU (Herb. Halácsy)).

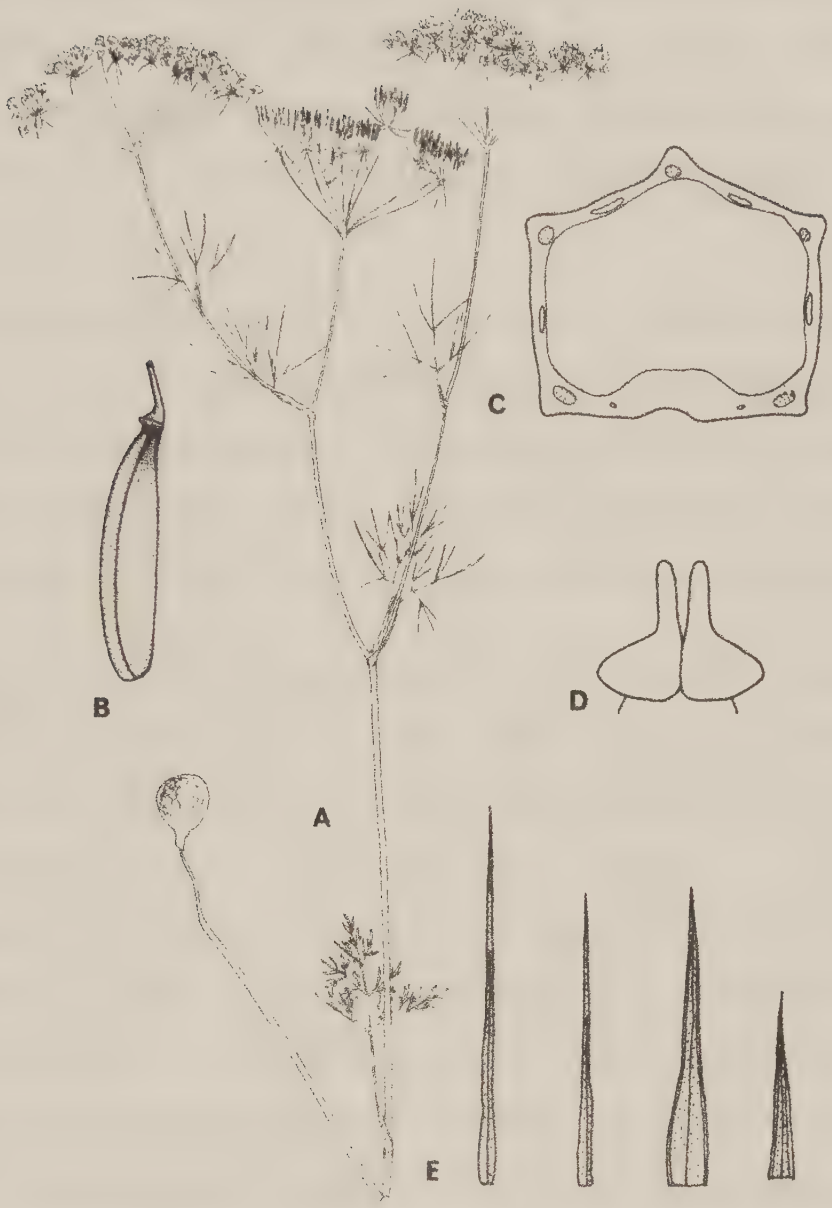


Fig. 18. Geocaryum capillifolium (2n=20). -- A: Habit (type 1 in text). -- B: Mericarp. -- C: Transverse section of mericarp. -- D: Sideview of stylopodium at anthesis. -- E: Bractlets. -- A: X0.5. -- B, E: X8. -- C: X40. -- D: X20.

Freyera montenegrina Baldacci 1901 p. 23. -- Freyera cynapioides B. montenegrina (Bald.) Hayek 1927 p. 994. -- Orig. coll.: Baldacci 1898. Iter Alb. (Montenegr.) sectum. Num. 80. Hab. in umbrosis ad jugum Sutorman et in m. Vrh-suta versus distr. Primorije et Crmnica. 6 Junio. (lectotype in BM, isotypes in W, WU).

Freyera pelia Beauverd & Topali 1937 p. 258--260. -- Orig. coll.: S. Topali et G. Beauverd, 13.6.1935. Hab. in collibus petrosis herbidisque supra Hagios Laventes in Mt Pelio Thessalie, c. 700-900 m non frequens, cum Asphodeline lutea, Salvia amplexicaule, Lathyro grandiflora, Dentaria bulbifera, etc, mixta. (holotype in G (Herb. Boiss.)). The sheet was not seen in Geneva.

Comments: In the original description of Myrrhis capillifolia Gussone mentioned several localities so that there should be several syntypes. Only the one mentioned has been traced. It has not been possible to get the specimen on loan from Napoli but its identity has been checked.

The combination Conopodium capillifolium (Guss.) Boiss. is incorrectly used for a Conopodium species in Spain and Portugal (e.g. in Flora Europaea 1968).

The type specimen of Freyera pelia, which in the original description is said to be in the Boissier Herbarium in Geneva, was not found there so that no material of the species has been seen. The description corresponds entirely to G. capillifolium. The drawing which accompanies the description is somewhat diagrammatic but not contradictory.

The original material of B. balcanica Vel. has not been traced. In the description Velenovský wrote that he had seen material of the species which was collected by Adamovic near Pirot. As neotype material from this locality has been chosen, also collected by Adamovic but one year after the publication.

Bunium capillifolium Kar. & Kir. of the Asiatic flora is a synonym of Scaligeria setacea (Schrenk) Korov.

Description: Erect, slender perennial. Tuber globose, in flowering indivi-

duals 5--10(--13) mm in diameter. Stem (20--)25--50(--55) cm, glabrous or with short hairs at the base. Underground part of stem short, 1--5 cm. Number of branches 0--3. Basal leaves triangular in outline, 3--4-pinnate, ultimate lobes 3--10(--15) mm long, lanceolate, petiole up to 15 cm long, usually shorter; leaves changing from the basal to the uppermost ones; upper cauline leaves 1--2-pinnate, rarely undivided, lobes linear to filiform, up to 40 mm long, 0.2--1.4 mm broad; petiole only a sheath, up to 10 mm long, usually shorter. Number of umbels 1--4; the terminal umbel with 5--13 rays; rays 10--30(--40) mm long, straight or curved like a swans' neck. Bracts lacking. Bractlets (3--)5--7(--8), linear-triangular or very narrowly lanceolate, 2.0--6.3 mm long, 0.2--0.7 mm broad. Petals white. Anthers white or greenish. Stylopodium white at anthesis. Pedicels with teeth at apex. Fruit black, linear-oblong, 2.7--4.5 mm long; ridges prominent; styles in fruit erect or slightly divergent; length of style and stylopodium (0.7--)0.8--1.2 (--1.9) mm; vittae one per interval, sometimes with two on commissure. Chromosome number 2n=10,20,(0--9)B. Illustration Figs. 18, 19.

Flowering period: May to July.

Distribution and habitat: G. capillifolium has the widest distribution of all species of the genus. It occurs in southern Italy, from Sicily northwards to Gargano. In southern and eastern Yugoslavia, from Crna Gora to Serbia and Makedonija. In Greece eastwards to Khalkidiki and Mt Athos and southwards to Mt Oité in Fthiotis. It is also found in Bulgaria near the border with Serbia. In N Albania and probably also in E Albania but no material or note in the literature has been seen from that area.

G. capillifolium usually grows in shady forests of Fagus and Quercus, often just at the edge of an opening, e.g. along a path. In C Greece Fagus and Quercus is replaced by Abies cephalonica. In Crna Gora the species is found in mountain meadows without trees or with thickets of Fagus sylvatica. These localities are very rich in herbs and grasses. The altitudinal differences are

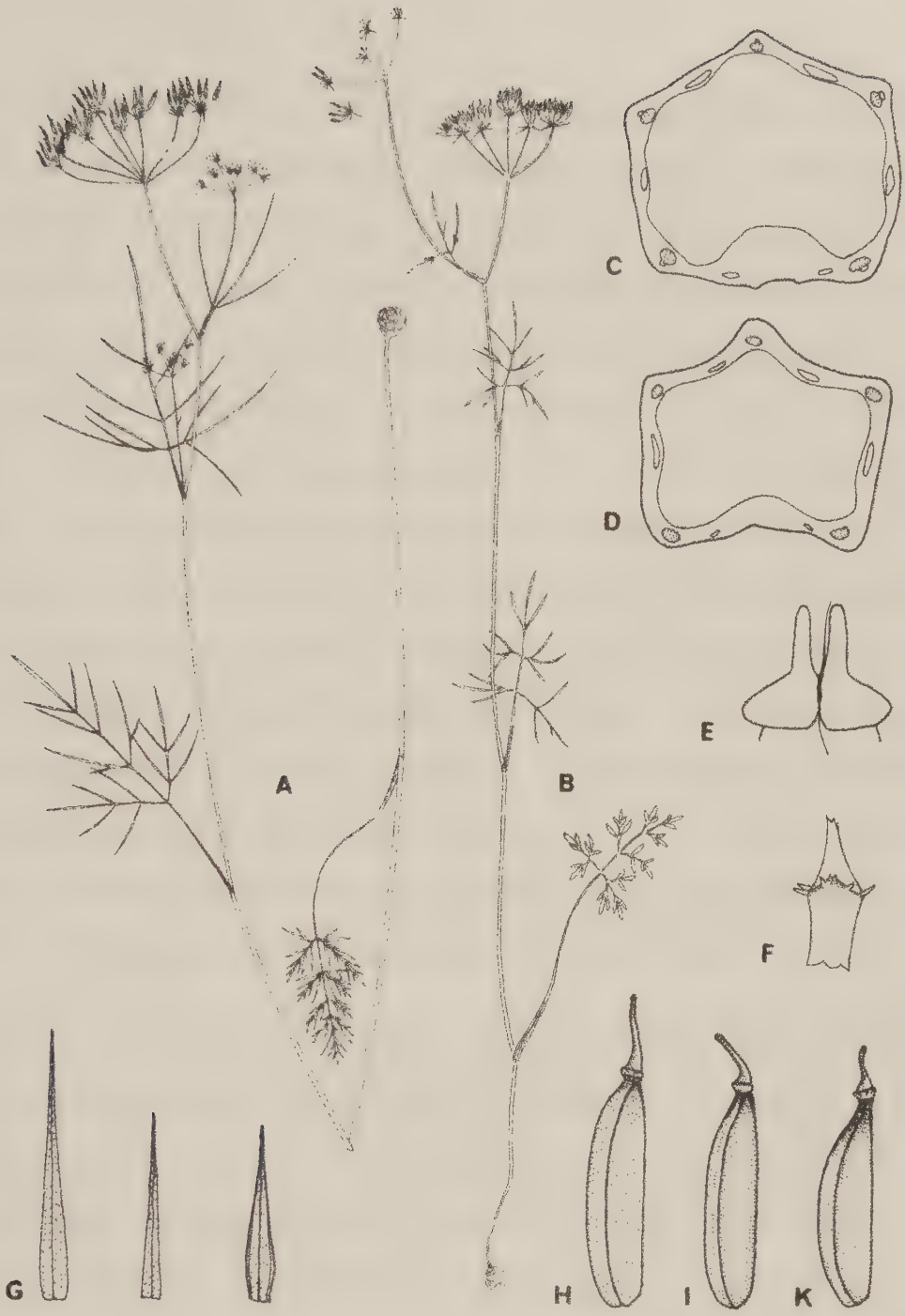


Fig. 19. Geocaryum capillifolium (2n=10). -- A: Habit (type 2 in text). -- B: Habit (type 3 in text). -- C: Transverse section of mericarp (type 2). -- D: Transverse section of mericarp (type 3). -- E: Sideview of stylopodium at anthesis. -- F: Apex of pedicel with part of carpophore. -- G: Bractlets. -- H, I: Mericarps of type 2. -- K: Mericarp of type 3. -- A, B: X0.5. -- C, D: X40. -- E, F: X20. -- G, H, I, K: X8.

considerable varying from c. 450 to 2100 m. Associated species found on Mt Oitē (E23) are: Abies cephalonica, Arrhenaterum elatius, Dactylis glomerata, Helleborus cyclophyllus, Lapsana communis, Secale montanum, Senecio rupestris, Silene saxifraga, Trisetum flavescens, Verbascum epizanthum var. samaritanii. Gargano represents the typical locality which occurs from S Italy to Mt Athos (E45): Asphodeline liburnica, Astragalus glycophyllus, Lathyrus niger, Melica uniflora, Orobanche sp., Physospermum verticillatum, Quercus cerris, Ruscus aculeatus, Scutellaria altissima, Stellaria holostea. The locality at Cakor (Crna Gora) is a mountain meadow with thickets of Fagus (E49): Anthoxantum odoratum, Anthyllis vulneraria, Asphodelus albus, Bellis perennis, Campanula patula, Carum carvi, Cerastium moesiacum, Cynosurus cristatus, Dianthus cruenthus, Fagus sylvatica, Fragaria moschata, Luzula silvatica, Lychnis viscaria, Orchis ustulata, Phleum commutatum, Pimpinella serbica, Plantago media, Poa pratensis, Polygala major, Potentilla recta, Primula elatior ssp. imbricata, Ranunculus bulbosus, Sanguisorba minor, Viola tricolor. (Fig. 17)

Variation and distinguishing characters: G. capillifolium has not only the widest distribution but also the widest variation. The pattern of variation may be graphically described as a triangle where the three corners represent a special type. Between the corners there are transitional forms so that it not has been possible to circumscribe any of them as a separate taxon. The three corner types are:

(1) In the cultivated material this type is represented by the collections E48, E49, E50, all from the C Balkan Peninsula; i.e. N Greece and S Yugoslavia from 1450 to 1800 m. It is characterized by the filiform lobes of the cauline leaves. The mean value of the breadth is less than 0.5 mm and the length is about 15 mm. The teeth of the pedicels are small. The somatic chromosome number is 20. This form corresponds well, but not entirely, with the collection made by Baldacci described as Freyera montenegrina.

(2) This type is represented by the collections E11, E45, E46, E47, E51, and is widespread in S Italy, S Yugoslavia and N Greece from 450--900 m. It is recognized by the leaf lobes which are about 1 mm broad and 18--30 mm long (mean values). The teeth of the pedicels are always conspicuous. The somatic chromosome number is 10. This form includes the type material of G. capillifolium.

(3) The third type is represented by the collection E23 from Mt Oitê. It is present in some mountains in C Greece always in Abies forest. It has smaller cauline leaves than type (1) and (2) and does not give the same impression of umbrageousness as the others. The teeth of the pedicels are usually conspicuous. The fruits are small, sometimes not more than 2.7 mm. The somatic chromosome number is 10. Material from Mt Timfristos has been described as Freyera congesta by Boissier and Heldreich.

Some material from S Serbia can most certainly be placed in type (1) but there are several collections from the surroundings of Niš which are difficult to define. Measurements of pollen grains indicate that the plants should be tetraploids (VI. Morphological variation). On the other hand the morphology shows that at least part of the material belongs to the diploid type (2).

In C and N Greece there are types which are morphologically transitional between (3) and (1) but also between (3) and (2). Conopodium graecum described by Freyn and Sintenis belongs to this group. Even within each of these groups there is local variation.

None of the three types have been given taxonomic rank as only some of the material seen can be definitely placed in any of them. Type (3) can probably be regarded as an ecotype adapted to the relatively dry conditions of the Abies forest in Greece. Type (2) is adapted to the deep shape and the moister conditions of a deciduous forest. Type (1) is a tetraploid, possibly with a certain preference for higher altitudes.

G. capillifolium is distinguished from G. tuberosum and G. cynapioides on the linear to filiform lobes of the cauline leaves and on the linear-triangular bractlets. The fruits are usually smaller. G. capillifolium is somewhat similar to G. stylosum, which, however, lacks pedicel teeth (see under G. stylosum).

GEOCARYUM PARNASSICUM (BOISS. & HELDR.) ENGSTR. COMB. NOV.

Freyera parnassica Boissier & Heldreich 1856. Diagn. Pl. Or. Nov. 3(2) p. 102. -- Biasolettia parnassica (Boiss. & Heldr.) Nyman 1865 p. 27. -- Butinia parnassica (Boiss. & Heldr.) Heldr. ex Nyman 1879 p. 302. -- Orig. coll.: Heldreich 1852. In monte Parnasso, Rarissima in reg. alpina. 11 Aug. (holotype in G (Herb. Boissier)).

Comments: Heldreich wrote the combination Butinia parnassica on a herbarium sheet in 1852.

Description: Erect, slender perennial with curved internodes. Tuber globose, in flowering individuals 8--23 mm in diameter. Stem (12--)15--30(--43) cm. Underground part of stem flexuose, up to 10 cm long. Number of branches 0--4, rarely with secondary branches, usually exceeding the terminal umbel. Basal leaves triangular in outline, 2--3-pinnate; ultimate lobes 3--7 mm long, c. 1.5 mm broad, lanceolate or narrowly elliptic, acute; upper cauline leaves consisting of a sheath and a linear to filiform undivided lamina, up to 20 mm long; leaf sheaths glabrous, very rarely ciliate. Number of umbels 1--5, very rarely more; terminal umbel with 4--7(--10) rays; rays (7--)13--35(--28) mm long. Bracts lacking. Bractlets (2--)3--6(--7), narrowly triangular or lanceolate, up to 4 mm long, 0.3--0.8 mm broad, often with reddish or white midvein and margin. Anthers yellow-green or pink. Stylopodium white at anthesis. Petals white. Apex of pedicels with teeth (absent in plants from Mt Taiyetos). Fruit

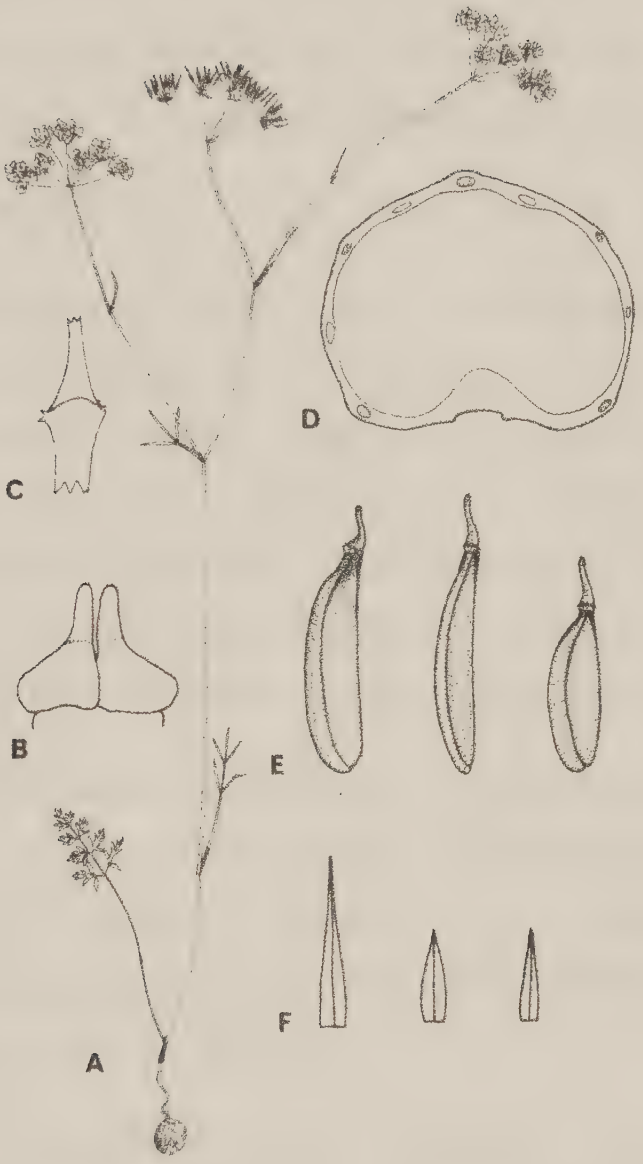


Fig. 20. Geocaryum parnassicum. -- A: Habit. -- B: Sideview of stylopodium at anthesis. -- C: Apex of pedicels with part of carpophore. -- D: Transverse section of mericarp. -- E: Mericarps. -- F: Bractlets. -- A: X0.5. -- B, C: X20. -- D: X40. -- E, F: X8.

black, linear-oblong, abruptly narrowed below stylopodium, 2.6--4.0 mm long; ridges not prominent but distinct; vittae one per interval, generally lacking on the commissuralside; styles erect or slightly divergent. Length of style and stylopodium 0.7--1.0 mm. Chromosome number 2n=10. Illustration Fig. 20.

Flowering period: May to July.

Distribution and habitat: G. parnassicum is distributed in mountains of S Greece, mainly in Peloponnisos from 1000 to 2300 m, generally at c. 1500 to 1800 m. Usually found in sheltered localities such as damp places just below cliffs or in Abies forests. From Mt Parnis (E5) the following associated species are noted: Abies cephalonica, Calamintha alpina, Centaurea mixta, Convolvolus elegantissimus, Cynosurus echinatus, Euphorbia myrsinites, Festuca laevis, Medicago lupulina, Sanguisorba minor, Sedum rubens. (Fig. 14).

Variation and distinguishing characters: G. parnassicum is not very variable. In general appearance the species is homogeneous but some populations may deviate in minor characters. A collection from Mt Xerovouna has very short and erect styles which are parallel and not pressed together. In plants from Taiyetos the pedicels are not toothed.

The species is best recognized by the slender stem with curved internodes. The upper cauline leaves have an almost filiform, undivided lamina. The fruits are small. On Mt Parnis G. parnassicum grows together with G. macrocarpum of the Imittos type which has divided laminas of the upper cauline leaves and pedicels which are thickened in fruit.

GEOCARYUM EUBOICUM (RECH. FIL.) ENGSTR. COMB. NOV.

Freyera euboica Rechinger fil. 1956. Anzeig. Akad. Wiss. (Wien) 93 p. 98. --

Orig. coll.: Rechinger fil. 1955 no. 16770. Euboea sept.: Montes Kandili, in silvis umbrosis (Abies ceph. et Pinus Pallasiana), substr. calc., c. 800--1000 m, 30.5. (holotype in W, isotypes in G, S).

Description: Erect, slender perennial with straight internodes. Tuber globose, not more than 10 mm in diameter. Stem 20--38 cm with more or less flexuose underground part, glabrous. Number of branches 0--1. Basal leaves triangular in outline, 2--3-pinnate; lobes broadly lanceolate-oblong, obtuse to apiculate, up to 4 mm broad, up to 10 mm long; upper cauline leaves 1--2--pinnate, lobes linear-lanceolate, acute, up to 3 mm broad, up to 30 mm long; leaf sheaths glabrous. Number of umbels 1 or two; terminal umbel with 4--7 rays; rays 10--20(--35) mm long, almost straight. Bracts lacking. Bractlets 2--5(--7), narrowly lanceolate to subulate, up to 5 mm long. Petals white. Apex of pedicels without teeth. Fruit black, linear-oblong, 3.6--4.8 mm long; ridges distinct but not prominent; styles recurved at maturity; vittae one per interval. Chromosome number not known. Illustration Fig. 21.

Flowering period: April.

Distribution and habitat: G. euboicum is known from a few collections on the mountains Kandhilion and Dhirfis on the island of Euboea (Greece). It grows in sheltered and shady places in forests from 750 to 1000 m. The collection E9 is from the S side of a ravine with a small stream shaded by Platanus. Other species found in this locality are: Abies cephalonica, Asplenium trichomanes, Helleborus cyclophyllus, Luzula forsteri, Melica minuta, Ophioglossum vulgatum, Platanus orientalis, Primula vulgaris, Pteridium aquilinum, Viola reichenbachiana. (Fig. 14).

Variation and distinguishing characters: G. euboicum is a uniform species. In the broad lobes it most closely resembles G. divaricatum from Mt Killini. G. euboicum is quite erect, unbranched or with one very short branch. The

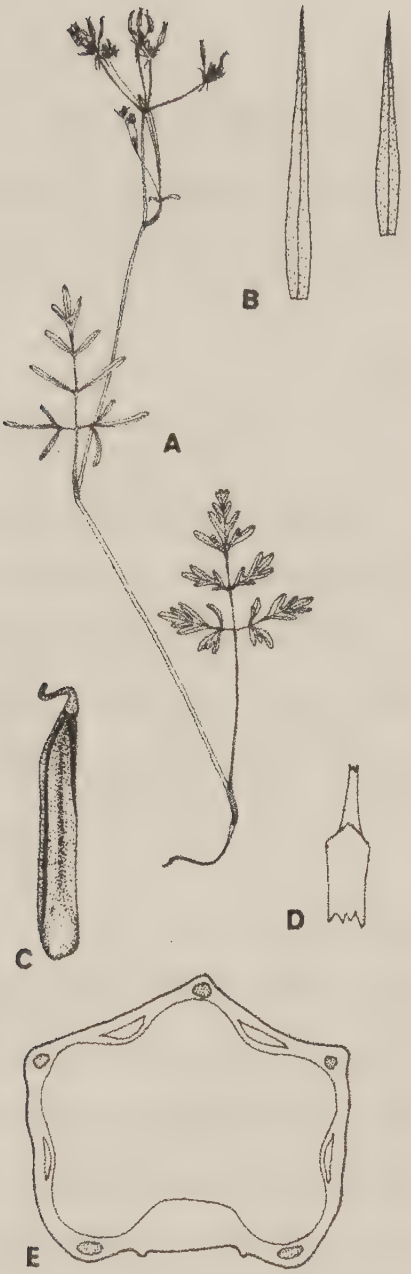


Fig. 21. Geocaryum euboicum. -- A: Habit. -- B: Bractlets. -- C: Mericarp. -- D: Apex of pedicel with part of carpophore. -- E: Transverse section of mericarp. -- A: X0.5. -- B, C: X8. -- D: X20. -- E: X40.

styles are recurved.

In the shape of the bractlets and the slender habit G. euboicum shows affinities to the diploid species. It is probably most closely related to G. parnassicum from which it is easily distinguished by the broad leaf lobes.

GEOCARYUM DIVARICATUM (BOISS. & ORPH.) ENGSTR. COMB. NOV.
Freyera divaricata Boissier & Orphanides 1856, Diagn. Pl. Or. Nov. 3(2) p. 102. -- Biasolettia divaricata (Boiss. & Orph.) Nyman 1866 p. 28. -- Huetia cynapioides subsp. divaricata P.W. Ball 1968 a p. 18. -- Orig. coll.: Orphanides 1852. In monte Kyllene prope Trikala (Haigios Vlasios), june 17, (holotype in G, isotype in WU (Herb. Halácsy)).

Description: Erect perennial with slightly curved internodes. Tuber globose? Stem 24--35 cm, glabrous, underground part flexuose. Number of primary branches 2--4, often with secondary and tertiary branches, axils up to 90°; middle cauline leaves triangular in outline, long-petiolate, 2-pinnate, lobes broadly lanceolate to oblong, obtuse to apiculate, up to 3 mm broad; upper cauline leaves reduced. Number of umbels up to 5; terminal umbel with 4--5 rays; rays 23--45 mm long, divaricate. Bracts lacking. Bractlets 1--3, 1.5--4.0 mm long, 0.5--0.8 mm broad, triangular to lanceolate. Apex of pedicels without teeth. Fruit black, lanceolate-oblong, 4.4--6.2 mm long, c. 1.7 mm broad, lanceolate--oblong, 4.4--6.2 mm long, c. 1.7 mm broad; ridges prominent; styles and stylopodium c. 1.5 mm long; styles slightly divergent; vittae small or lacking at maturity. Chromosome number not known. Illustration Fig. 22.

Flowering period: May, June.

Distribution and habitat: G. divariacatum is only known from Orphanides'

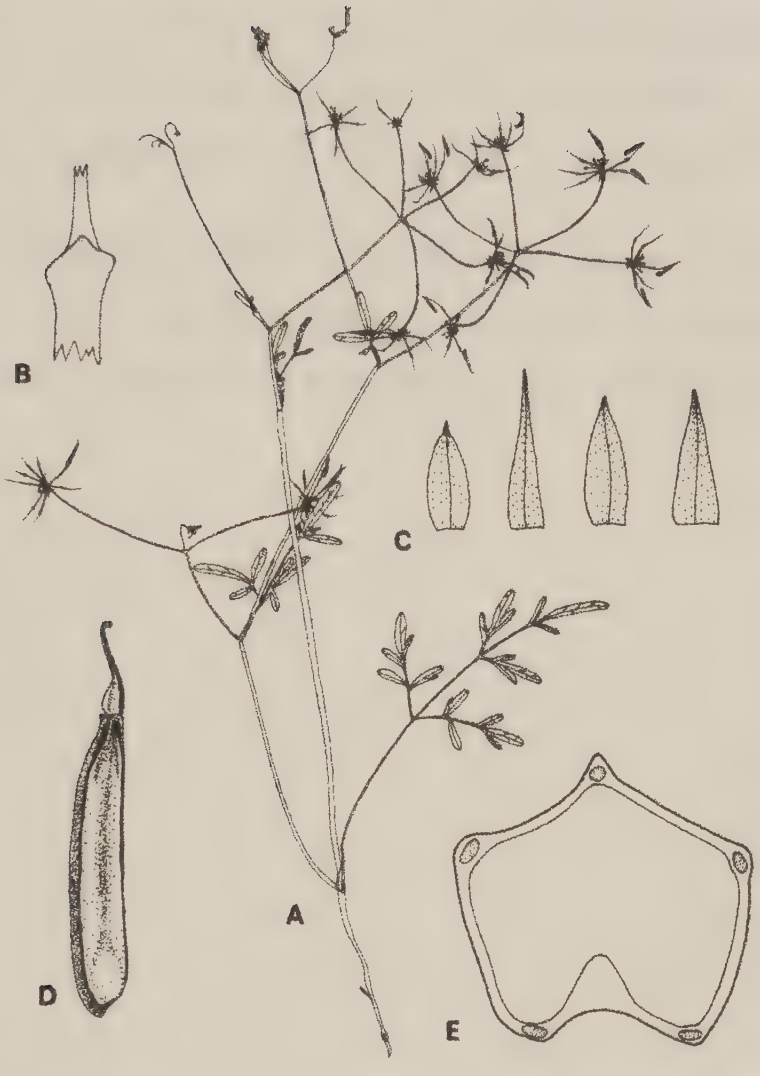


Fig. 22. Geocaryum divaricatum. -- A: Habit. -- B: Apex of pedicel with part of carpophore. -- C: Bractlets. -- D: Mericarp. -- E: Transverse section of mericarp. -- A: X0.5. -- B: X20. -- C, D: X8. -- E: X20.

single collection from Mt Killini in N Peloponnisos. The only specification of the locality given is "prope Trikala". The village of Trikala is situated at an altitude of c. 1000 m. That should mean a rather sheltered locality fairly rich in herbs, bushes and trees. Such places around Trikala have been searched twice by the author but the species was not found. (Fig. 14).

Variation and distinguishing characters: The only collection is uniform. G. divaricatum has the broad leaf lobes in common with G. euboicum but is distinguished by the number of branches and the only slightly divergent styles.

IV. CYTOLOGY AND BIOLOGY

CYTOLOGY

Aims

No cytological investigations have previously been carried out on Geocaryum. No chromosome numbers have been published except those in Engstrand (1973).

The primary aim of this study was to determinate the chromosome numbers in different taxa of the genus. Owing to the moderate size of the chromosomes it has not been possible to make a more detailed analysis of their morphology.

The value of cytological data is very restricted in Umbelliferae. Most workers have almost entirely dealt with chromosome numbers, one good exception being the work on Bupleurum by Cauwet (1967, 1968). Runemark (1968 b) could use the chromosome numbers, and to some extent also the chromosome morphology, in the taxonomy of Tordylium.

Methods

For chromosome counts the plants were pretreated for c. 12 hours at 2--4^{o} C. Root tips were fixed in the Svalöv modification of Navashin-Karpechenko. The root tips were sectioned at 12 μm and stained in 1% crystal violet and 1% aniline solution (1:1).

For the study of chromosome morphology the material was treated as follows: Long root tips (c. 3 cm) were treated in 2mM 8-hydroxyquinoline for c. 24 hours at 2--4° C and then fixed in Carnoy (3:1). The tips were stained and squashed in a 3% solution of acetorcein.

Studies on meiosis were made on a few plants by fixing yound buds in Carnoy. The anthers were stained and squashed out in a 3% solution of acetorcein.

All material was collected in nature as tubers and cultivated in the Botanical Garden, Lund.

Chromosome numbers and morphology

In all 288 individuals from 55 collections have been examined. (see Table 3). Three different chromosome numbers have been found, 2n=10, 18 and 20.

A detailed analysis of the chromosomes was difficult as they are small and very similar. They vary in size from 1--3 µm. Only exceptionally is it possible to identify pairs of homologues. The chromosomes are metacentric to submetacentric to subtelocentric (terminology according to Levan et al. 1965). In the diploid species there is a pair of chromosomes with satellites. These chromosomes are two of the longest in the complement. They are submetacentric to subtelocentric. The centromeric position varies somewhat in different plates, even from the same individual. However this is most certainly due to technical difficulties such as those described by Bentzer et al. 1971. In material with small chromosomes there can be even greater errors in the arm ratio than those described by Bentzer et al. The authors' opinion is that the projection of the chromosome pictures onto paper by means of a camera lucida causes most of the errors. These facts can also explain the differences in size of the satellites. They are usually smaller than the rest of the short arm to which they are localized but are sometimes about the same size. In the karyotypes no pairing of the homologues has been made except for the satellites (Fig. 23).

In the tetraploid species (2n=20) 2 pairs of satellite chromosomes have been

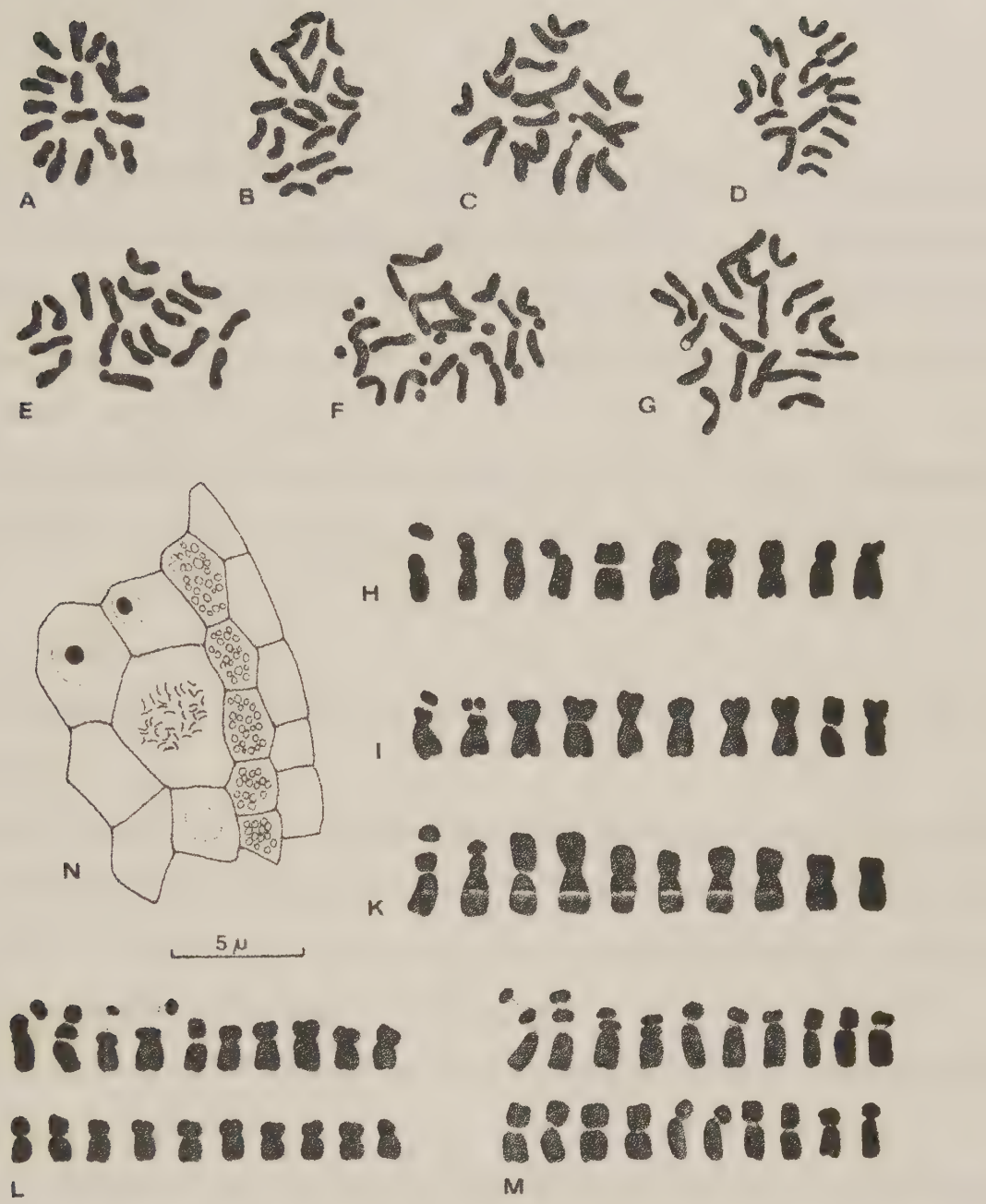


Fig. 23. A--G: Somatic metaphases in sections of root tips. -- H--M: Squash technique. The chromosomes are arranged more or less after their length. -- N: The position of an endomitotic cell in a section of a root tip. -- A: G. cynapioides (E44). -- B: G. pindicola (E25). -- C: G. pumilum (E26). -- D: G. peloponesiacum (E16). -- E: G. tuberosum (E53). -- F: G. capillifolium 2n=20 (E49). Note nine B-chromosomes. -- G: G. macrocarpum (E7). -- H: G. parnassicum (E28). -- I: G. capillifolium 2n=10 (E46). -- K: G. capillifolium 2n=10 (E23). -- L: G. macrocarpum (E8). -- M: G. macrocarpum (E65). -- N: G. pindicola (E22). The scale is not suitable for N.

identified with certainty in only some of the material of G. stylosum and G. macrocarpum. It must, however, be mentioned that it is only in very good preparations that all 4 satellites are found so that no certain conclusion can be drawn from the fact that in G. tuberosum with 2n=18 only 1 pair of satellite chromosomes has been found.

With the difficulties described above it is natural that no differences can be observed in the karyotypes of taxa of the same chromosome level.

B chromosomes

Supernumerary chromosomes have been observed in G. capillifolium and G. tuberosum.

In the former species 2 B chromosomes were found in the diploids (E47:9). Out of 29 individuals of tetraploid G. capillifolium 2 had B chromosomes. The plant E49:12 had 9. In collection E53 of G. tuberosum (2n=18) 25 individuals were examined and 6 plants were found to have 1, 2 or 4 B chromosomes.

Owing to technical difficulties it was never possible to study these plants with the squash technique.

All B chromosomes are of similar appearance. They are almost sphaerical with a diameter of less than 0.5 µm. (Fig 23 F).

B chromosomes are extremely rare in Umbelliferae. There are c. 900 species which have been cytologically examined. Of these Dethawia tenuifolia (Ram. ex DC.) Gordon has been reported to have 2n=22 (+4B) (Favarger & Huynh 1964). Nothing is stated about the morphology of these B chromosomes. Weimarck (unpubl. data) has found supernumerary chromosomes in Heracleum.

Endomitosis

Endomitosis, in this case the formation of large cells containing twice as many chromosomes as usual, has been found in 6 plants representing G. macrocarpum, G. pindicola, G. peleponnesiacum, G. cynapioides, tetraploid G.

Table 3.

Results of the cytological investigation.

Species	Coll. nr.	Number of ind.	Chrom. nr.	Endomit. obs. or not	Number of B chrom.
macrocarpum	E1,2,3,4, 6,7,8,10, 65,94,97	38	20	+-	0
stylosum	E66,68	2	20	-	0
pumilum	E26,27	10	20	-	0
creticum	E19,20	6	20	-	0
peloponesiacum	E12,13,14, 15,16,17, 55,57,62	38	20	+-	0
pindicola	E21,22,24, 25	29	18	+-	0
cynapioides	E44	5	18	+-	0
tuberosum	E52,53	37	18	+-	0;1;2;3
capillifolium	E11,23,45, 46,47,51	69	10	-	0;2
capillifolium	E48,49,50	30	20	+-	0;1;9
parnassicum	E5,28,29, 30,31,32, 54,56,58, 60,61,63	24	10	-	0

capillifolium and G. tuberosum. These have the chromosome numbers 2n=18 and 2n=20. Endomitosis has not been found in any diploid species. In this material the endomitotic cells were found in the peripheral parts of the root sections (Fig. 23 N). In 1 plant there were endomitotic cells in 3 successive sections of a root tip. They were in exactly the same position indicating that there was a vertical row of endomitotic cells in the root tip.

It has not been possible to find any reports of endomitosis in Umbelliferae. However, it is not uncommon in other material. According to Gustafsson (1973) endomitotic cells are present in almost every individual of the Atriplex triangularis group.

Cytologically deviating individuals.

In the material studied only two individuals were found to be cytologically deviating.

In a section preparation of G. macrocarpum (E7:4) one of the longest chromosomes was observed to have a clear constriction in one of the arms (Fig. 23 G). It was not possible to trace the origin of the constriction but it probably had a great effect on meiosis as this plant was the only one found to have diminished pollen fertility with only 57% stainable pollen (see under Male fertility).

In a plant of G. stylosum from Samos (E68:8) a case of aneusomaty (Duncan 1954) was found. Most cells in a squash preparation had 20 chromosomes but in 4 cells 21 could be counted with certainty. None of the chromosomes had a morphology which could suggest it to be a B chromosome like those found in G. capillifolium and G. tuberosum.

Meiosis

Meiosis was examined in only a few plants of G. pumilum, G. peleponesiacum, and G. pindicola. In these plants meiosis was normal.

MALE FERTILITY

The calculation of the percentages of morphologically good pollen grains is intended to give an estimation of fertility. It can be assumed that unstained pollen grains do not germinate on the stigma and that it is a product of disturbed male meiosis. This is probably not true in every case but nevertheless the percentages of good pollen may be an indication of disturbances at meiosis. The pollen grains were stained with cotton blue. Unstained pollen grains were always malformed in one way or another. Between 200 and c. 450 grains were counted from each plant. In some of the material pollen fertility was calculated on three different occasions. If the plants had a high percentage of good pollen the variation was usually very slight, normally only a few per cent variation being found. The material was collected in the field as tubers and cultivated in the Botanical Garden, Lund.

In all 189 individuals were examined, representing G. stylosum, G. macrocarpum, G. pindicola, G. parnassicum, G. pumilum, G. peleponesiacum, G. creticum, G. tuberosum, both cytotypes of G. capillifolium, and G. cynapioides (Table 4). 146 individuals had more than 96% morphologically good pollen, 20 individuals had less than 90% good pollen and only 1 individual had less than 75%. This plant was found to be heterozygous for a constriction (see under Cytology).

No differences could be traced between collections, perhaps partly due to the limited material.

It is of course difficult to understand the biological consequences of reduced pollen fertility. Gustafsson (1973) uses the expression "reduced fertility" for plants under 90%, meaning that below this the reproduction of the plant really could be effected. This seems to be a reasonable supposition. In 5 taxa of Atriplex triangularis group Gustafsson found reduced fertility in c. 10% of the material, almost exactly the same amount as found in Geocaryum. Theoretically a great reduction in fertility is more dangerous for annuals such as Atriplex than for perennials. It could more easily affect the size of

Table 4

Pollen fertility (%) in some selected collections and in the whole material.

Species	Coll. nr.	50	60	70	80	90	100	n
pindicola	E22					2	9	11
capillifolium, 2n=20	E49					2	9	11
tuberosum	E53					1	9	10
stylosum	E66				1	1	22	24
	E67					1	17	18
whole material			1		2	17	169	189

a population. The possibilities for perennials to tolerate "genetic load" has been stressed by Stebbins (1950). In Artemisia vallesiaca Persson (1973) found that only a few per cent of the individuals had a pollen fertility between 90 and 100%. Normally the percentage of good pollen was 75--80. In Anemone nemorosa Bothmer et al. (1971) found that c. 70% of the clones investigated were below the limit of 90%.

Geocaryum has a limited duration whereas Artemisia and Anemone nemorosa can propagate vegetatively. As regards fertility Geocaryum is more likely to be compared to annuals. Nevertheless Geocaryum must be considered to have a high level of fertility.

GENETIC STABILITY

The investigation of cytology and male fertility has shown that Geocaryum is genetically stable as regards structural changes. If structural changes exist they do not greatly affect meiosis as almost all the material is highly fertile. It is true that only marked structural changes would have been revealed with the methods used. This has been demonstrated for instance in Leopoldia (Bentzer 1972) where the chromosomes are larger and structural heterozygosity can more easily be studied.

Geocaryum is found to be predominantly autogamous and Müntzing (1954) stated that structural heterozygosity is less common in self-fertilizers than in outcrossing plants.

Nothing is actually known about the mutation rate of the plants. The formation of tetraploids and aneuploids has increased the possibility of forming new gene combinations. Polyploidy is known to have had a role in the evolution of Umbelliferae. Moore (1971) calculated that c. 25% of the genera show interspecific variation in chromosome numbers.

CROSSING EXPERIMENTS

Method

The first difficulty of the crossing experiments is connected with cultivation. It was not possible to follow a hybridization plan because the plants it had been intended to use rarely flowered at the same time. So the crossing experiments had to be improvized during the period of anthesis.

First as many flowers as possible of an umbel were emasculated on one or two occasions. All other flowers were removed and the emasculated flowers were isolated in a pergamin bag. However, this method was clearly injurious to the plant. The best way was to emasculate the flowers successively during 2 to 6 days and to perform the pollination during the same time. The plants used as female parents were kept separate from those used as male parents. The female plants had to be checked and emasculated twice a day.

Experiments were also made with emasculation without pollination. In these cases most of the ovaries developed quite normally at the beginning. They looked fresh and reached 2.5--2.9 mm. After two weeks many ovaries began to desiccate and after c. 20 days all had atrophied. The longest were c. 4 mm.

Results

In Table 5 are listed the different combinations of crossings performed and the number of mericarps produced. It must be kept in mind that the number of flowers pollinated varied greatly. In all 156 seeds were produced but only 6 of these germinated.

All combinations of crossings within G. macrocarpum have resulted in seed setting. The intrapopulational cross E1:16 X E1:4 (Naxos) gave rise to a plant as did the interpopulational cross E10:1 X E6:3 (Pelagos X Imittos). None of these hybrids produced seed after self-pollination. In the first cross the pollen fertility was 97% and in the second 44%. Three interpopulational crosses in G. pindicola also resulted in hybrid plants. They all had a high pollen

Table 5.

The combinations in which hybridization experiments have been carried out and the resulting seed setting.

Intrapopulational crosses

Female	Male	Seeds
E1:16	E1:4	14
E52:2	E52:27	-
E53:8	E53:27	-

Intraspecific crosses

Female	Male	Seeds	Female	Male	Seeds
E1:1	E10:8	1	E46:4	E23:3	-
E10:1	E6:3	13	E46:6	E11:10	-
E10:4	E1:7	5	E48:1	E50:2	5
E10:7	E4:4	4	E52:8	E53:17	-
E10:8	E2:1	26	E53:22	E52:11	-
E12:6	E55:1	-	E53:30	E52:18	-
E24:2	E22:9	26	E65:5	E36:2	-
E24:12	E22:9	2	E66:8	E67:4	-
E46:1	E51:6	41	E67:3	E66:5	-

Interspecific crosses at the same level of chromosome number

Female	Male	Seeds	Female	Male	Seeds
E10:2	E26:6	-	E66:20	E48:8	-
E22:20	E13:5	1	E66:20	E25:4	-
E25:8	E17:3	-	E66:30	E49:13	-
E27:6	E16:8	18	E67:13	E21:1	-
E44:1	E52:23	-			
E49:44	E67:4	-			

Crosses at different levels of chromosome numbers

Female	Male	Seeds
E49:18	E11:11	-
E52:9	E49:3	-
E52:22	E22:11	-

fertility but there where considerable differences in fruit setting after self-pollination. One plant produced c. 89% of the possible number of mericarps in the terminal umbel and the other 2 0% and c. 3%.

One interspecific hybrid between G. pindicola and G. peloponesiacum has been obtained. The pollen fertility was c. 93% and the percentage of seeds obtained c. 10%. (Table 6).

In the artificially produced hybrids there is no connection between pollen fertility and the number of seeds produced. It should be noted that in wild plants the percentage of possible number of mericarps is 100 or almost 100 after self-pollinations.

In a combination of G. pumilum and G. peloponesiacum 18 seeds were obtained but did not germinate. Interpopulational combinations in G. capillifolium also produced seeds, which, however, did not germinate.

No seeds were produced in any combination where G. tuberosum and G. stylosum were involved, not even when the plants used originated from the same population.

Of the 35 possible crossing combinations only 6 yielded hybrid plants. In spite of the high pollen fertility only one cross produced a higher percentage of seeds. Of the 35 crossing experiments c. 20 involved G. stylosum and G. tuberosum but no hybrid was obtained.

REPRODUCTIVE ISOLATION

Hybridization in Umbelliferae

Natural hybridization in Umbelliferae is rare and very few putative hybrids have been examined in detail. Shan & Constance (1951) and Bell (1954) have

Table 6.

Pollen fertility and percentages of possible number of mericarps in artificially produced hybrids.

Intrapopulational crosses	E1:16 X E1:4	97.4	0
intraspecific crosses	E10:1 X E6:3	44.0	0
	E24:2 X E22:9	98.5	2.9
	E24:2 X E22:9	98.5	88.7
	E24:12 X E22:9	93.5	0
Interspecific crosses	E22:20 X E13:5	92.7	10.3

found that hybridization in combination with polyploidy has played a considerable part in the evulotion of the Sanicula crassicaulis complex and thus produced allo- and autoalloploids. Hybridization within the genus Aciphylla from New Zealand is reported to be frequent. Wardle (1963) regards this as the result of a recent and rapid evolution of the mountain flora. The sterile hybrid of Apium inundatum and Apium nodiflorum, Apium X moorie (Syme) Druce occurs where the two species grow together. Beuzenberg & Hair (1963) have studied natural hybrids of Apium in New Zealand. Reese (1969) has reported a natural hybrid between Eryngium campestre and E. planum. These species have different chromosome numbers. Sourková (1972) found a specimen of Bupleurum which, on morphological grounds, is presumed to be a hybrid between B. falcatum and B. longifolium. It is quite clear that hybrids of umbelliferous plants are very rarely found in nature. One reason could be that in many genera the differences between species are so slight that hybrids would hardly be recognized. Many of the larger European genera, such as Seseli, Peucedanum, Pimpinella and Laserpitium are characterizied by regional and local species which are effectively isolated by reason of geographical and ecological differences, which in fact is presumed to be the reason for the taxonomic difficulties in these groups. The same system is present in Geocaryum.

Isolation mechanisms in Geocaryum

The crossing experiments indicate that genetic barriers have developed between most populations but also between certain individuals within a population. However, these barriers are of different strength as some combinations yield seeds and even hybrids. Hybridization between established populations cannot be of importance in the evolution of the species and in fact no plants have been found which could be suspected of being hybrids. The germination of the hybrid seeds must be considered together with the germination difficulties of seeds. (See II. Morphology and general description).

Such sterility barriers between individuals and populations support the theory of self-fertilization and probably, to some extent, pollination between certain individuals in populations. The cited example with frequent hybridization in Aciphylla shows that such a system does not hold for the whole family.

As the Geocaryum species are confined to islands or mountains the spatial isolation of species and populations is pronounced. Furthermore several of the species grow under different ecological conditions. There are also differences in the flowering periods (see under Taxonomy). These are consequences of the differences in ecology so that under cultivation late-flowering alpine plants start flowering earlier than plants from lower altitudes.

POLLINATION

Geocaryum and probably all other Umbelliferae belong to a group of plants which are pollinated promiscuously (Grant 1949) by unspecialized insects. Through the visual impact of the flowers the whole umbel acts as a single blossom (Faegri & van der Piji 1966). When an insect crawls over the inflorescence it will spread pollen over the whole umbel.

The flowers are described under II. Morphology and general description. The stamens move in a special way during anthesis (Fig. 3). They are alternate to the petals and are enclosed by these in the bud stage. When the bud begins to open the filaments stretch and at the same time bend backwards. In the species G. capillifolium, G. tuberosum and G. cynapioides the movement ceases when the stamens are in a plane parallel to the petals. In the other species the movement continues until the stamens are pointing downwards and the filaments are parallel to the ovary. At this stage, when the stamens are bent backwards and the petals are pointing outwards, the styles are optimally exposed for pollination. The anthers are not open so that, if cross-pollination does occurs it

is more likely to do so at this stage. However, a central flower of the umbel may well receive pollen from a peripheral flower as anthesis starts at the periphery.

The stamens arise one at a time and reach just beyond the styles when the anthers are opened. If the flower has not been fertilized earlier it will most certainly be selfed at this stage. After anthesis the stamens are excurved under elongation of the filaments.

Protandry is very common in Umbelliferae (Drude 1898, Bell 1971). But no indication of protandry has been found in Geocaryum. Some male flowers have small styles and rudimentary ovaries but functional female parts have never been observed.

The only opportunity for cross-pollination to occur seems to be during the short time when the styles are optimally exposed. All species of Geocaryum which have been cultivated have been found to be completely self-compatible. As there is a mechanism favouring self pollination the conclusion is that this is the dominant mode of fertilization.

REPRODUCTION AND DISPERSAL

There is no indication of asexual propagation in Geocaryum. As seen under VI. Morphological variation, there are considerable differences in seed setting between populations. G. cynapioides was found to have the highest number of seeds in the terminal umbel. In G. capillifolium the tetraploid population produced more seeds than the diploid ones. In G. stylosum plants from one population produced almost twice as many seeds as plants from another. The number of seeds differs somewhat in cultivation mostly owing to modifications in the percentages of hermaphrodite flowers, but as far as could be checked the

trends were the same. If the size of a population is to remain unchanged e.g. G. cynapioides, needs a higher reproductive capacity than G. stylosum. Thus G. cynapioides must either have more difficulty in establishing new individuals or are shorter lived.

Geocaryum can be spread by tubers or by seeds. Spreading by means of tubers may be of some importance for the vertical distribution on a mountainside. The tubers follow with the screes downwards and establish at lower altitudes. G. peloponesiacum and G. pindicola in particular have been observed to grow in vertical lines which are the result of this movement. It can be assumed that plants can survive for long periods even at low altitudes, as the lower screes are well drained and there is no competition from other species. This may explain the wide modificative diversity found in G. peleponesiacum from Mt Panakhaikon.

The dry, rather stiff styles prove an effective means of dispersal. In some groups, viz. G. euboicum, G. creticum and in the Parnis and Imittos populations of G. macrocarpum the styles are recurved. The mericarps of the last group fasten easily in clothes and must also fasten in the wool of sheep and the fur of other animals.

The toothed fruit ridges, which are found in some of the material of G. pumilum are probably of positive value for dispersal (Fig. 9).

STRUCTURE OF POPULATIONS

G. macrocarpum is found on several Aegean islands, in southern Turkey and in Attiki. In Turkey the populations are very large, consisting of many thousands of individuals (Runemark, personal communication). On Aegean islands there is a lack of suitable localities. The populations of Rodhos and Naxos are

large but split up in clusters between which gene exchange could at least theoretically take place vicinistically. The population of Tinos consists of perhaps only 50--100 individuals. Each island is completely isolated. G. stylosum has a population cluster similar to that of G. macrocarpum on Rodhos and Naxos.

The species of the pumilum-pindicola complex are confined to alpine and high mountain areas of Crete, Peloponnisos and C Greece. The species grow mainly in screes and on landslides which are generally well separated. Each such locality is inhabitated by only 10--50 individuals. Many such localities are probably completely isolated while others are part of a population cluster. The same applies to G. parnassicum but it grows in different habitats and often forms larger populations.

The northern, erect species (G. tuberosum, G. cynapioides, G. capillifolium) grow mainly in deciduous forests, often in great numbers. The largest population found was that of tetraploid G. capillifolium at Cakor, Yugoslavia, the population consisting of hundreds of thousands of individuals. The plant is one of the dominants in montane and alpine meadows. Normally each part of a population cluster of the erect species is confined to some hundreds of individuals. These species are not limited by a lack of suitable localities as is G. macrocarpum for instance.

V. CHEMICAL VARIATION

THIN-LAYER CHROMATOGRAPHIC INVESTIGATION

Material and methods

This is an investigation to show the presence or absence of non-identified leaf substances extractable in HCl-methanol. The method is, with minor alterations, that described by Weimarck (1970). It will only be briefly described here.

Tubers collected in nature were planted in the open in the Botanical Garden, Lund. Basal leaves were collected in the morning and dried and stored under uniform conditions. 20 mg dry leaf tissue from each plant was macerated and extracted for 18 hours in 0.3 ml methanol with c. 1% HCl. The glass plates were prepared according to Nybom (1963). 20 mg of the cellulose powder was suspended in 120 ml distilled water. The run length was 90 mm in direction I and 130 in direction II.

10 µm of extract was applied at the starting point. The plates were arranged as the "multiple sandwich chamber" described by Weimarck (1970) and Nybom (1964).

The run in direction I was performed in a jar containing 2% formic acid in distilled water. For direction II a mixture of amyl alcohol, glacial acetic

acid and distilled water in the proportions 22:13:11 was used. Before the final drying the plates were dipped in a solution of a phenolic reagent (diphenylboric acid ethanolamine complex). The spot pattern was studied in UV light, Fluo test, 360 nm. Each extract was double tested.

Aim

The aim was to investigate whether thin-layer chromatography could yield any information on the taxonomy of the genus and to get a picture of intra- and interpopulational variation.

Treatment and evaluation of the spot pattern

Each spot is characterized by colour and by its Rf-values. The Rf-values given in Table 7 represent mean values and there is a certain amount of variation so that the relative positions of the spots are also of value in identification.

Altogether there are 30 spots in the material. They can be divided into three groups. The first group consists of spots 1--9. They are all yellow with a low value for Rf I. Although situated close to one another in one row they are easily found and identified and can be accorded great significance. Identification is facilitated by the characteristic gaps between spots 2 and 3 and between spots 8 and 9. (See Fig. 24).

The second group consists of the blue and blue-green spots 10--20. They are well-spread over the plate and are also easily identified. Spots 13 and 15 are sometimes poorly separated.

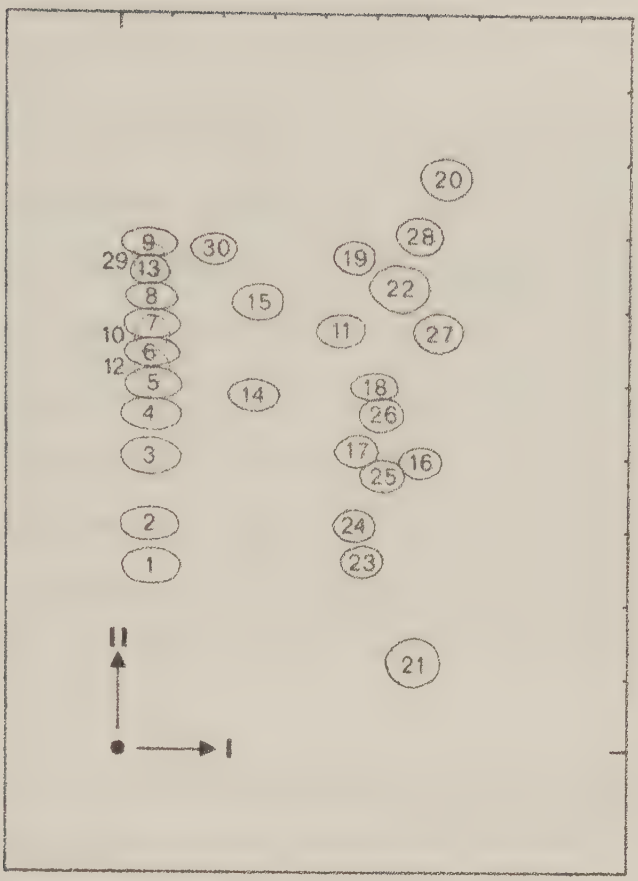
The third group consists of the violet spots 21--30, which are also well spread over the plate. With one exception (spot 22) they are difficult to see and are often overlooked. They must be considered of very little significance.

Each extract has been tested on two plates. Some of these failed but double tests are available for 201 individuals. Only six spots do not differ in any

Table 7.

Characteristics for the spots.

Spot nr.	Colour	RfI	RfII	Presence in percentage of collections	Presence in percentage of individuals	Frequency of differing double tests
1	yellow	.06	.24	10	3	17
2	"	.08	.30	56	70	4
3	"	.07	.40	100	100	0
4	"	.06	.45	100	100	0
5	"	.06	.50	59	53	9
6	"	.06	.54	83	70	1
7	"	.06	.58	26	12	22
8	"	.05	.61	26	15	15
9	"	.04	.68	28	11	48
10	light blue	.06	.57	23	37	13
11	"	.43	.57	100	99	0
12	blue-green	.05	.52	13	26	0
13	"	.04	.64	100	100	0
14	"	.26	.49	59	58	12
15	"	.27	.63	100	100	0
16	"	.56	.39	3	3	57
17	"	.48	.41	74	71	4
18	"	.51	.50	95	60	5
19	"	.45	.66	43	59	18
20	"	.64	.79	8	2	50
21	dark violet	.59	.12	3	4	33
22	"	.56	.63	77	84	0
23	violet	.49	.26	10	7	47
24	"	.48	.30	77	54	34
25	"	.52	.38	10	6	57
26	"	.51	.46	5	4	20
27	"	.62	.57	54	25	40
28	"	.59	.70	77	54	44
29	"	.04	.66	5	3	67
30	"	.17	.66	5	3	83



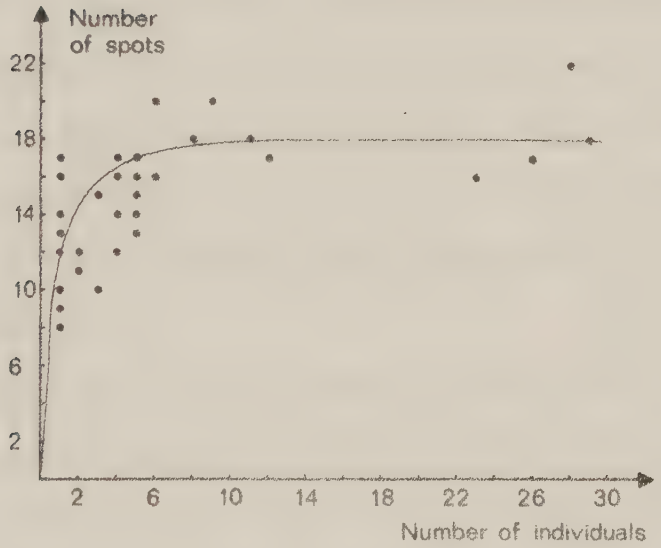


Fig. 24. Above: Master key to the spots. -- Below: Number of individuals examined and number of spots found in each collection. The curve is somewhat approximative (see further in text).

double test. If a spot is found in only one of the two plates it has, of course been 'registered' as present in the individual. For each spot it has been calculated in how many percentages this happened of the total number of individuals where the spot occurs. A high number signifies that the spot is easily overlooked and should be accorded little significance. All the violet spots (except no. 22) have high values (see Table 7) and are almost ignored when judging the spot patterns. High values are also found in spots 9 and 16.

Some spots are present in all individuals examined (see Table 7). They may be characteristic of the genus but are of no value when the aim is to study variation.

In order to get an adequate picture of the spot pattern of a population it is necessary to study a certain number of individuals. The diagram in Fig. 24 shows that, up to a certain limit, the total number of spots found in a collection increases with the number of individuals examined. The diagram is a mixture of populations of several species but the curve should be different in different taxa depending on their degree of heterogeneity and the total number of spots. Nevertheless at least 6--8 individuals should be examined before one can expect to have found all spots. However the spots could still be found in new combinations.

When discussing the spot patterns it can be practical to separate the spots into stable and sporadic spots. Stable spots occur in all individuals of a collection while sporadic spots occur at varying frequencies.

The results of chromatographic experiments are often evaluated by statistical methods as when the material is very extensive and difficult to survey. Most of the statistical methods have decided disadvantages and have been adversely criticized (e.g. Weimarck 1970, 1974, Runemark 1968 a).

I have chosen to present the chromatographic experiments a graphical account by means of staple diagrams. However, as with numberical methods the result must be judged subjectively. In order to study the exact intrapopulational

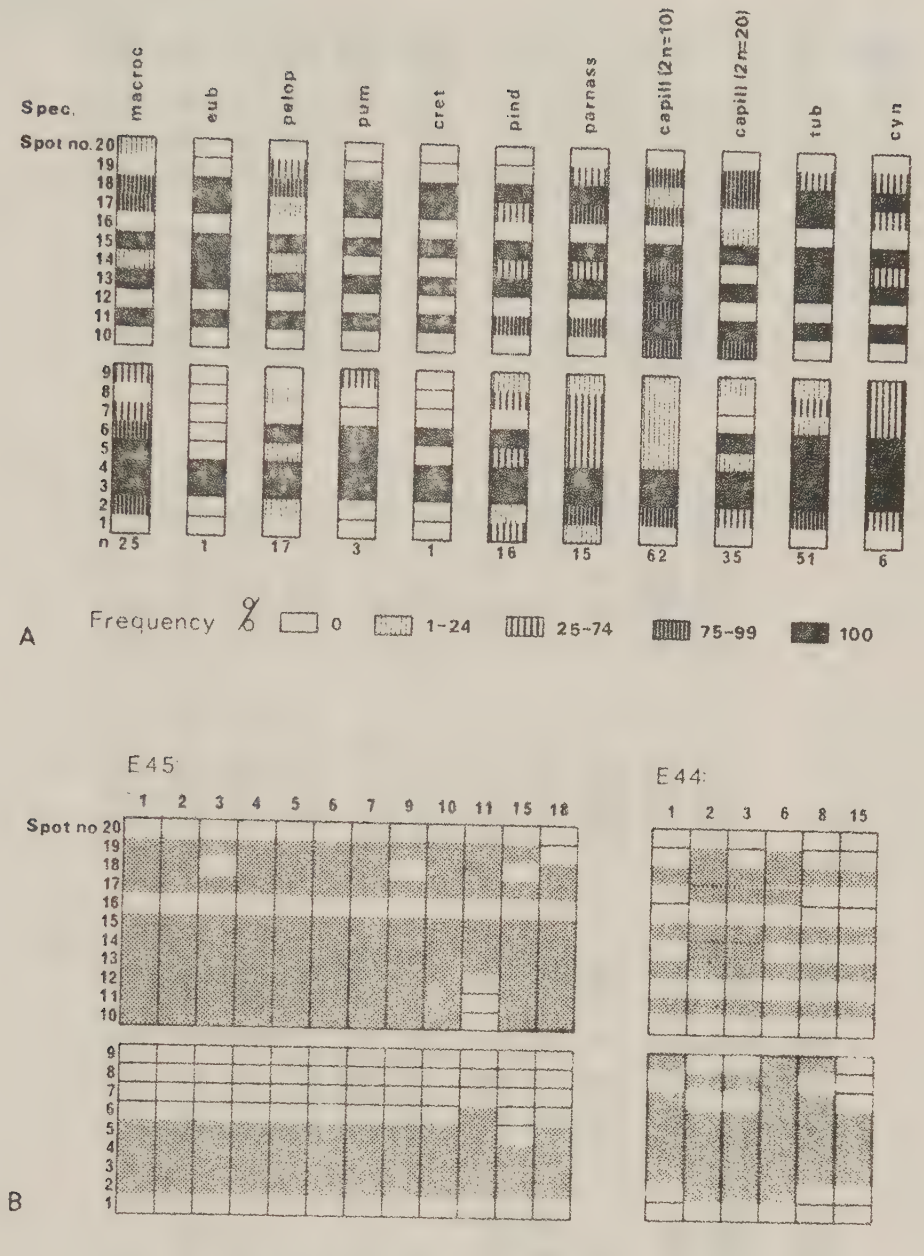


Fig. 25. Staple diagrams showing the occurrence of the spots nos. 1 -- 20. -- A: Frequency of the spots in the species and the two cytotypes of G. capillifolium. All individuals examined are included. -- B: Intrapopulational variation in E45 (G. capillifolium) and E44 (G. cynapioides). Presence (dotted) and absence (white) are marked for each individual.

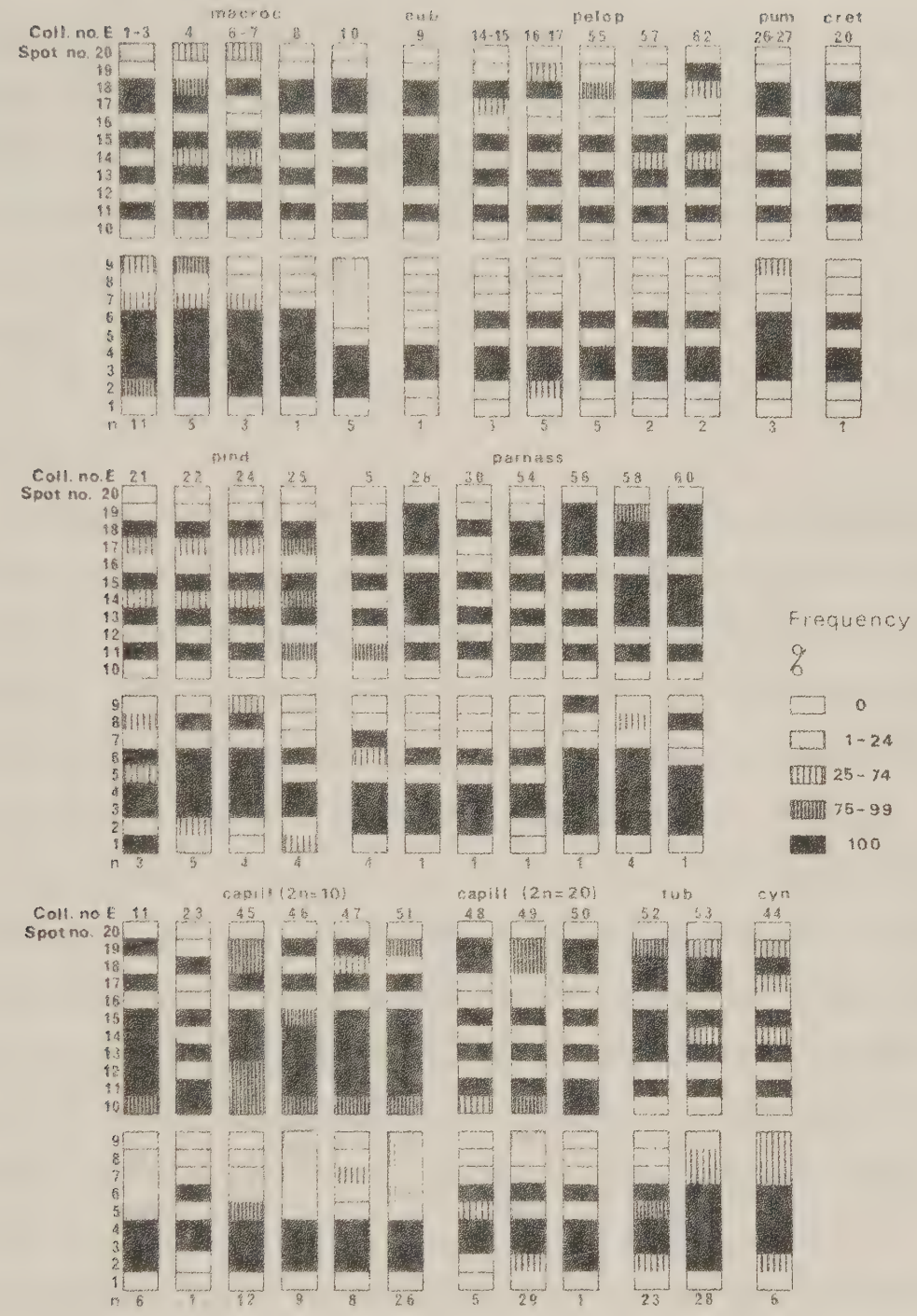


Fig. 26. Staple diagrams showing the occurrence of the spots nos. 1 -- 20 in the examined collections. The diagrams are arranged in species and cytotypes.

variation each individual is represented by a staple where the presence or absence of each spot is marked by different symbols (Fig. 26). At the same time each such staple gives information on the intrapopulational variation. Corresponding diagrams have been constructed for the species (Fig. 25 A).

As the violet spots (21--30) are of very little significance they have been excluded.

Results

Two examples of exact intrapopulational variation have been presented in Fig. 25 B. Collection E45 represents a fairly constant population where 4 individuals of 12 deviate in 1 or more spots. In E44 2 individuals of 6 are similar. In other populations it has been noted that if an individual deviates it often does so in 2 or more spots (e.g. coll. E46). It should be noted that not a single collection is constant as regards spots 1--20.

G. macrocarpum is represented by 5 populations. Spot 20 is unique for the species but occurs only sporadically in material from Naxos, Tinos and Imittos. The collections E1--3 and E4 are very similar but differ in spot 18 which is stable in E1--3 but sporadic in E4, and in spot 2 which is stable in E4 and sporadic in E1--3. The collections E6--7 deviates in lacking spot 17 which is stable in all other collections. The same applies to E10 as regards the spots 5 and 6.

G. peloponesiacum is represented by 5 collections none of which has been sufficiantly examined. There is no spot which is unique for the species. The differences between the populations lie mainly in the frequencies which is also true of G. peloponesiacum as compared with G. pumilum and G. creticum.

G. pindicola has the almost unique spot 1. It occurs in all populations except coll. E24 but also in a single individual of G. parnassicum (coll. E32, not presented in Fig. 26). G. pindicola is variable as regards spots 1--9 but fairly constant in the others. G. parnassicum is represented by 9 populations

(7 only presented in Fig. 26) but with very little material. The variation between populations is considerable but no conclusions can be drawn an account of the limited material investigated.

The two cytotypes of G. capillifolium have the unique spot 10 in common, but it occurs only as a sporadic one. Most diploid forms are separated from the tetraploids by the presence of the stable spots 17, 14, and the partly stable spot 12. The tetraploids have the stable spot 6 which is missing or sporadic in the diploids. However, it should be noted that the single individual examined in collection E23 is similar in all these details to the tetraploids. E23 (Mt Oiti) is the only diploid examined which belongs to type 3 of G. capillifolium described in III. Taxonomy. Except for the presence of spot 10 the Oiti material is also similar to the diploid G. parnassicum.

The two collections of G. tuberosum, E52 and E53 are interesting because they have both been sufficiently examined. These collections could be compared to E44 of the closely related G. cynapioides. E53 and E44 have the three spots 7, 8, and 9 in common as sporadic ones while these are totally lacking in E52. In all other spots these three collections differ only in frequencies. E.g. spot 14 is stable in E52 but sporadic in E53 and E44. In the same way spot 17 is stable in E52 and E53 but sporadic in E44.

Discussion

The investigation provides no definite answers to taxonomic problems in the genus Geocaryum but confirms the concepts of several species founded on results of other methods.

G. capillifolium is a heterogeneous species with two cytotypes and three morphological types (see III Taxonomy). The occurrence of the unique, sporadic spot 10 in all populations examined supports the decision to unite these types in a single species. On the other hand diploids belonging to type 2 differ from the tetraploids in several spots. It has been shown that a population

should be represented by at least 6--8 individuals to be sufficiently examined. However, a single individual from a population may be valuable when it is compared with well-investigated populations as with the individual from the collection E23 which belongs to the capillifolium-type 3. It cannot be very similar to diploids of type 2 because in those spots 2 and 17 are stable but it may well be similar to the tetraploids as it differs only by the absence of spot 19, which is sporadic in the well-investigated collection E49.

In the case of G. tuberosum and G. cynapioides there is no evidence of specific delimitation. In some spots E53 of G. tuberosum resembles E44 of G. cynapioides rather than the other tuberosum collection E52.

As a method chromatography is in this case more valuable in studies of intra- and interpopulational variation. There is considerable intrapopulational variation in the material and no population where more than one individual has been studied is constant. The variation between populations of the same species is largely a question of different spot frequencies. There are some striking exceptions as in G. macrocarpum where spot 17 is absent in E6--7 and spots 5 and 6 are absent in E10. Those spots are stable in E1--3 which has been well investigated.

The type of variation found in the chromatographic experiments is similar to the morphological variation. Few characters or spots are unique for a species and when this is so they are often sporadic and not present in all individuals. Among morphological characters with this type of variation the toothed pedicels can be mentioned. All populations of G. capillifolium have toothed pedicels although the teeth may vary in size. It is also typical for G. tuberosum, but teeth are lacking in some collections from Hercegovina. Toothed pedicels may also occur in individuals of G. peloponesiacum but are lacking in most material. Among quantitative morphological characters the size of the fruits and length of leaf lobes vary in the same way.

This obviously irregular occurrence of characters has greatly contributed to the taxonomic confusion within Geocaryum.

VI. MORPHOLOGICAL VARIATION

SIZE OF TUBER

Tubers collected in nature displayed considerable differences in size. The size of the tuber depends on several factors, the most important being age and the genetical possibilities, but the effects of these could be modified by environmental conditions such as the nutrient content of the soil.

Tubers in cultivation increased c. 2--5 mm in diameter in one season but the amount of growth differed in different individuals. The highest value observed was 9 mm. Many tubers did not increase in size at all.

The tubers were collected in populations which are presumed to be very old. Thus the distribution of ages ought to be well balanced. The samples were selected from flowering individuals so that one-year-old plants are not included in most collections.

The mean and the minimum--maximum of the diameter is presented for 40 collections of 11 species in Table 8. In 22 collections the minimum is 4--7 mm which should be about the size when flowering starts, although this may differ between populations.

The widest range of variation, 4--38 mm, and the highest mean, 24.5 mm, is found in collection E22 of G. pindicola. The largest tubers are often irregular

Table 8.

Diameter of tubers (mm) in spontaneous material.

Species	Coll. nr.	M	Min.	Max.	n
macrocarpum	E1	13.1	8	12	13
	E2	12.6	8	15	8
	E3	16.4	12	22	7
	E4	11.7	7	18	7
	E6	21.8	14	28	7
	E7	17.4	14	20	7
	E8	15.8	10	21	10
	E10	13.3	10	20	11
	E65	25.0	19	30	7
stylosum	E66	10.8	4	18	59
	E67	9.0	6	14	46
	E68	10.2	7	17	10
pumilum	E26	9.7	4	15	21
	E27	11.1	8	15	7
creticum	E19	11.4	7	18	8
	E20	10.8	7	17	11
peloponesiacum	E12	18.0	13	21	5
	E13	12.8	7	20	5
	E14	10.4	4	15	8
	E15	13.0	10	19	7
	E16	17.4	11	35	10
	E17	11.6	4	20	20
pindicola	E21	16.1	7	20	11
	E22	24.5	4	38	15
	E24	12.1	9	19	15
	E25	15.9	9	23	11
cynapioides	E44	8.6	4	18	20
tuberosum	E52	13.4	8	25	35
	E53	16.4	12	20	35
capillifolium, 2n=10	E11	12.7	10	17	19
	E23	4.9	4	7	23
	E45	9.5	5	15	21
	E46	8.9	6	12	17
	E47	11.1	6	15	17
	E51	8.1	4	12	41
capillifolium, 2n=20	E48	7.1	4	9	18
	E49	8.9	5	13	50
	E50	7.1	5	10	8
parnassicum	E5	14.6	8	23	10
euboicum	E9	7.7	4	12	14

Fig. 27. Diameter of tubers. -- E66, E67: G. stylosum. -- E23: G. capillifolium of type 3 (see taxonomy). -- E51: G. capillifolium of type 2. -- E49: G. capillifolium of type 1. -- E52, E53: G. tuberosum.

in shape and it is not quite correct to measure the diameter. Tubers from E22 did not grow faster than others in cultivation so that environmental factors can be presumed to have caused the large size. In the area where the collection was made there is a net-work of sheep tracks and the great number of sheep must have increased the nutrients in the soil.

Independent of ploidy level G. capillifolium has small tubers. The minimum values of the populations are almost identical. The collection E11 has a mean of 12.7 mm and a variation range of 10--17 mm. This collection does not even overlap with collection E23 which has a mean of 4.9 and a variation range of 4--7. As there are no small tubers in E11 the collection could be a non-representative sample of the population or younger individuals could be lacking. In the same way the largest tubers could have been missed when sampling E23 though this does not seem to be the case as the diagram shows (Fig. 27).

Fig. 27 shows the sizes in some populations of G. stylosum, G. capillifolium, and G. tuberosum. These diagrams could also be used to show the distribution in age in the populations (non-flowering plants excluded). In particular the collections E51 and E49 have almost the same number of individuals on both sides of the maximum. Generally there is a tendency to stretch out in the direction of the older plants which means that most plants of a generation die within a certain time after the mode age but that single individuals can live longer.

It has earlier been mentioned that one of the reasons for needing a higher potential capacity of reproduction is a shorter length of life. The highest reproductive capacity was found in E44 and E49 and the lowest in E46. Very little or no correlation can be found between seed-producing capacity and distribution of age unless the absolute age varies greatly in the populations.

Table 9

Size (cm) from the tuber to the uppermost umbel. Interpopulational variation in some erect species. Spontaneous material.

Species	Coll. nr.	M	Min.--max.	n
tuberosum	E44	44.9	34.0--52.0	9
cynapioides	E52	41.1	33.0--57.5	20
	E53	58.1	34.0--67.0	20
capillifolium, 2n=10	E45	45.6	34.0--57.0	17
	E46	42.9	34.5--52.5	12
	E47	38.6	30.5--47.0	13
	E51	46.4	27.5--59.5	20
capillifolium, 2n=20	E49	39.6	25.5--52.0	20
stylosum	E66	28.5	20.0--38.0	50
	E67	25.6	17.0--49.0	50

Table 10

Size (cm) from the tuber to the uppermost umbel. All spontaneous material available.

Species	M	Min.--max.	n
macrocarpum	23.6	13--45	51
stylosum	28.0	17--50	123
bornmuelleri	51.4	31--75	11
pumilum	8.7	3--17	59
peloponesiacum	11.9	2--30	56
creticum	7.1	3--12	19
pindicola	19.0	7--35	106
cynapioides	36.4	20--52	35
tuberosum	44.7	18--84	146
capillifolium	43.4	23--79	252
parnassicum	25.3	12--43	89
euboicum	26.8	20--38	8

Table 11

Number of branches from the stem. Variation between collections of four erect species. Spontaneous material.

Species	Coll. nr.	Number of branches 0	1	2	3	n	M
	E44						
tuberosum	E52	1	13	6		20	1.3
	E53	9	6	5		20	0.8
capillifolium, 2n=10	E45	6	7	2	2	17	1.0
	E46	4	7	1		12	0.8
	E47	2	6	5		13	1.2
	E51	1	6	12	1	20	1.7
capillifolium, 2n=20	E49	1	8	9	2	20	1.6
stylosum	E66	22	20	7	1	50	0.7
	E67	19	19	12		50	0.9

Table 12

Number of primary branches. Some localities of G. peloponesiacum. Spont. mat.

Locality	Number of primary branches 0	1	2	3	4	5	n	M
Panakhaikon		1	11	3		2	17	2.5
Kefallinia	1	2	1				4	1.0
Killini		3	9	4	1		17	2.2
Aroania		1	2	3	2		8	2.8

Table 13

Number of primary branches. All spontaneous material seen.

Species	Number of primary branches 0	1	2	3	4	5	n	M
macrocarpum		8	29	10	3		50	2.2
stylosum	42	45	29	4	2		122	1.0
bornmuelleri		1		5	5		11	3.3
pumilum	1	19	43	5	1		69	1.8
peloponesiacum	1	7	23	10	3	2	46	2.3
creticum		6	11	1		1	19	1.9
pindicola	9	27	52	11	1		100	1.7
cynapioides	2	8	16	8			34	1.9
tuberosum	20	55	63	13			151	1.5
capillifolium	32	99	84	26	3	2	246	1.5
parnassicum	10	26	38	13	2		89	1.7
euboicum	5	2					7	0.3

SIZE OF PLANTS

The size of the plants has been measured from the tuber to the top of the uppermost umbel and in the non-erect species, does not correspond to the length of the above-ground stem. These species usually have a long, flexuose underground part of the stem which is included in the measurements.

The means and the minimum-maximum values are presented in Tables 9 and 10.

NUMBER OF BRANCHES

Secondary branches

Secondary branching varies with the species. In the erect species G. capillifolium, G. cynapioides, G. tuberosum, and G. stylosum secondary branches are very rare whereas they are present in almost all individuals of G. bornmuelleri. They are also common in G. peloponesiacum, plants from Mt Aroania in particular being much branched. In G. pumilum, G. creticum and G. pindicola secondary branches can be found but are not common, and this is also true of G. macrocarpum. In G. parnassicum they are common but small.

It has been observed that it is the well-branched species that generally develop 2, or even 3 equal stems from the tuber.

Primary branches

The number of primary branches in the different species is presented in Table 13. The three species of the Aegean group are well separated from one another. Almost all plants of G. bornmuelleri have 3 or 4 branches the mean being 3.3. In G. macrocarpum almost 60% of the plants have two branches (mean 2.2). The mean value for G. stylosum is 1.0 with 71% of the individuals having 1 primary branch or none.

In the pumilum-pindicola complex G. peloponesiacum is outstanding with a mean of 2.3. However, in all species two branches are developed in 50--62% of the individuals. Plants of G. peloponesiacum from the island of Kefallinia have very few branches (Table 12).

The two species G. cynapioides and G. tuberosum never develop more than 3 branches. In G. capillifolium only 2% of the individuals develop more than 3 branches. Of these 3 species G. cynapioides has the highest mean value, 1.9.

In a study of populations of the erect species (Table 11) the G. cynapioides collection E44 has a mean value of 2.4 which is much higher than the two collections of G. tuberosum studied. G. capillifolium shows wide interpopulational variation. In the collection E46 the mean is 0.8 while that of E51 is 1.7. The tetraploid collection falls within the range of the diploids.

SHAPE OF LEAVES

The shape of basal leaves has been studied in G. capillifolium, G. tuberosum and G. cynapioides in particular. Measurements (Fig. 29 to the left below) and figures have been made on cultivated material. The values are means for collections. Where possible basal leaves from 20 individuals have been studied (Table 14).

The two cytotypes of G. capillifolium are distinct as regards the type of basal leaves. (Figs. 28, 29, 30). The diploids have longer basal segments than the tetraploids, so that the leaves are triangular. The ratio a/b is distinctly less in the diploids. The stalk (the part without lobes) of the basal segments is about twice as long in the diploids, i.e. the ratio b/c is less in the diploids than in the tetraploids.

There is some intrapopulational variation in these characters but little overlapping. As seen in the figures there is also wide intrapopulational varia-

Table 14.

Measurements of basal leaves (mm). Mean values of collections. -- a: Length of lamina, from the basal segments to the top. -- b: Length of basal segments. -- c: Length of stalk of basal segments. See also Fig.29, to the left, below. Cultivated material.

Species	Coll. nr.	a	b	c	a/b	b/c
G. capillifolium, 2n=10	E45	53.1	39.0	14.0	1.36	2.66
	E46, E47	51.0	36.6	12.5	1.39	2.99
	E51	42.4	29.8	11.0	1.42	2.70
G. capillifolium, 2n=20	E48	43.3	26.3	6.3	1.65	4.17
	E49	38.4	22.8	6.5	1.68	3.51
G. tuberosum	E52	59.8	42.1	19.8	1.42	2.23
	E53	54.0	38.1	14.6	1.42	2.80
G. cynapioides	E44	44.8	28.5	9.3	1.57	3.34

Fig. 28. Basal leaves. G. capillifolium (2n=20) coll. E49. Cultivated material.

Fig. 29. Basal leaves. -- Above: G. cynapioides coll. E44. -- Below: G. capillifolium (2n=10) coll. E45. Cultivated material. a, b and c are the measurements mentioned in text.

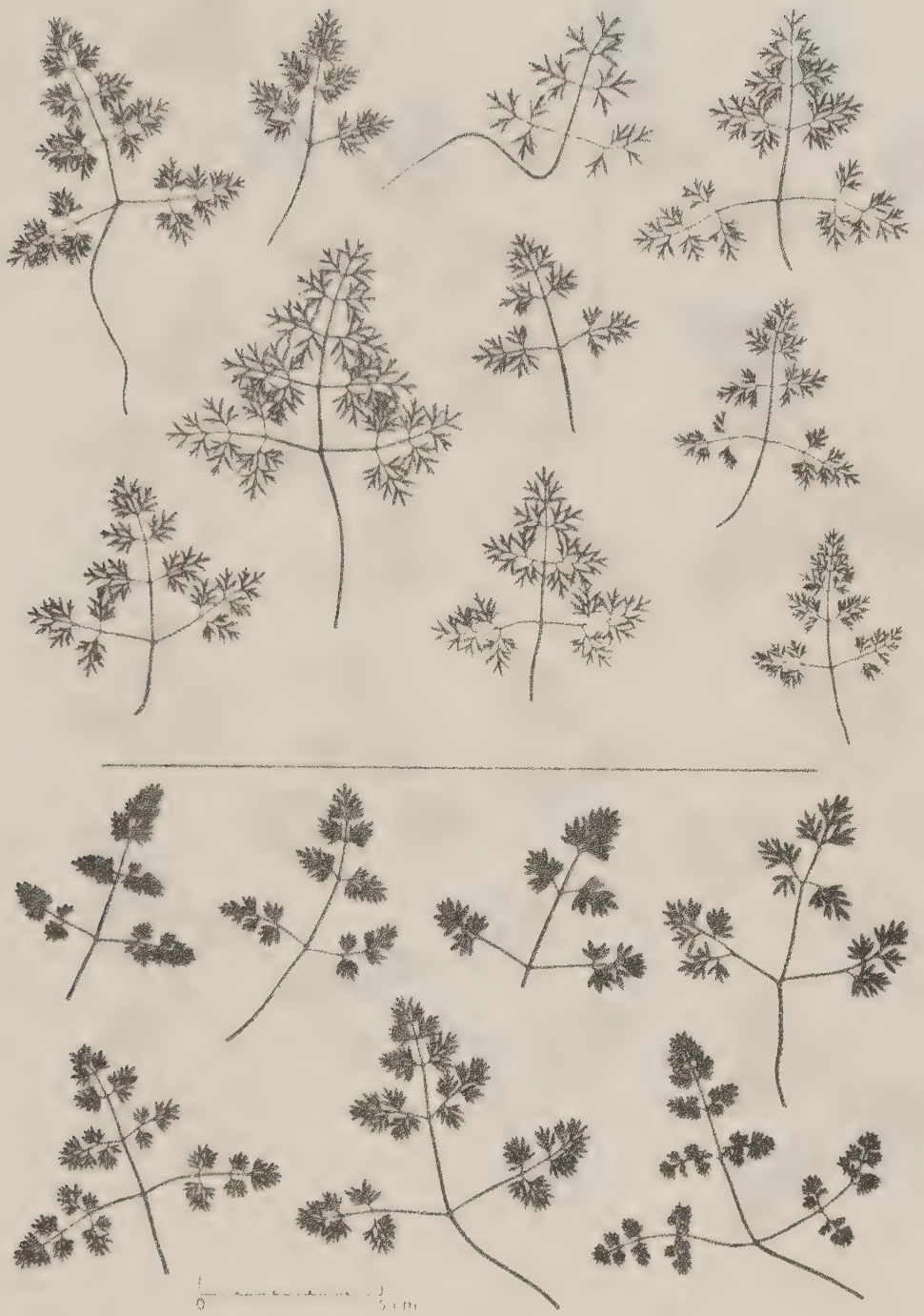


Fig. 30. Basal leaves. -- Above: G. capillifolium (2n=10) coll. E51. -- Below: G. tuberosum coll. E52. Cultivated material.

Fig. 31. Basal leaves. G. tuberosum coll. E53. Cultivated material.

tion in size of the leaf lobes and in the mode of incision of the leaves.

G. tuberosum and G. cynapioides can also be distinguished on the basal leaves.In Table 14 the values for G. tuberosum are very similar to those for diploid G. capillifolium, while those of G. cynapioides resemble the tetraploid. G. tuberosum can be separated from both G. cynapioides and G. capillifolium on the lobes which in a marked way are crowded towards the tops of the segments which is most evident in the collection E53 (Fig. 31).

The shape of the lobes of the cauline leaves is of taxonomic importance especially in the erect species. The cauline leaves of G. capillifolium and G. stylosum generally have linear to filiform lobes while those of G. tuberosum and G. cynapioides are more or less lanceolate. Measurements on wild material were made on the uppermost lobe of the second cauline leaf from the top.

In diploid G. capillifolium the lobes are about 1 mm wide and in tetraploids about 0.5 mm. The minimum to maximum values in E51 (diploid) are 0.6--1.6 and in E49 (tetraploid) 0.3--0.8. In this character G. stylosum is very similar to tetraploid G. capillifolium. In collection E53 (G. tuberosum) the width varies from 0.5 to 1.3 mm, mean 0.9 mm. The lobes of G. tuberosum are never more than 6 mm so that the ratio length/width is about 4 while in G. capillifolium and G. stylosum it varies from 26 to 40.

LENGTH OF PEDUNCLE OF TERMINAL UMBEL

The length of the peduncle is of little taxonomic interest in the erect species (Table 16). There are differences between the means of the populations investigated but the distribution is wide usually with no distinct mode and overlapping occurs.

In the pumilum group material from five localities of G. peloponesiacum has been examined (Table 15). There are considerable differences between localities

Table 15.

Length of peduncle of the terminal umbel (mm). Variation between some localities of G. peloponesiacum and between the species of the pumilum group. Spontaneous material.

Species	Locality	M	n	Min.--max.
peloponesiacum	Panakhaikon	27.0	17	0.0--66.0
	Kefallinia	20.9	4	14.5--26.5
	Taiyetos	14.6	10	0.0--26.5
	Killini	16.7	14	0.0--41.0
	Aroania	30.2	6	13.0--56.0
pumilum	Parnassos	5.5	64	0.0--31.0
creticum	Crete	17.5	14	3.5--45.0

Table 16.

Length of peduncle of the terminal umbel (mm). Variation between some collection of different species. Spontaneous material.

Species	Coll. nr.	M	n	Min.--max.
cynapioides	E44	39	12	16--58
tuberosum	E52	47	20	27--81
	E53	44	20	7--72
capillifolium, 2n=10	E45	35	15	20--50
	E46	36	14	27--52
	E47	41	13	15--67
	E51	43	20	28--82
capillifolium, 2n=20	E49	42	20	25--64
stylosum	E66	28	50	0--60
	E67	39	50	14--72

(e.g. between Taiyetos and Aroania). However, the type of variation is the same as that found in the erect species. Note that material from Panakhaikon covers the whole range of distribution found in the species. Only G. pumilum deviates significantly in this character. The mean value is extremely low, only 5.5 mm, and c. 80% of the individuals have peduncles between 0 and 7 mm long.

LENGTH OF RAYS IN THE TERMINAL UMBEL

The rays in a terminal umbel are measured (to the nearest millimeter) and the individuals represented by the means. Rays of secondary umbels are usually shorter.

A survey of the material is presented in Tables 17 and 18 in size classes. The means given have been calculated from exact measurements.

Although there is wide intrapopulational variation several populations are distinct. The two collections E52 and E53 (Table 18) (G. tuberosum) differ from each other but E52 is almost identical with collection E51 of G. capillifolium. In the erect species there are differences between populations but little or no difference between species.

In the pumilum group plants of G. peloponesiacum from four localities have been examined. This comprises all material seen from each mountain. The plants from Killini differ in having shorter rays.

All three species of the pumilum group have a wide range of variation and almost completely overlap. Nevertheless the means differ significantly from one another.

NUMBER OF RAYS

The rays have been counted in the terminal umbel. Other umbels, where

Table 17

Length of rays in terminal umbel (mm). Mean per umbel. Variation between some localities of G. peloponesiacum and between the species in the pumilum group. Spontaneous material.

Locality/ Species	2	4	6	8	10	12	14	16	18	20	22	24	26	28	38	40	n	M
Panakhaikon			1	2	1	2	1	4	2	3			1				17	14.3
Taiyetos				1	1	4	3					1					10	12.0
Killini		2	4	1	3	2	4			1							17	9.4
Aroania				1		2	1	2	1				1				8	14.2
peleponesiacum		2	5	5	5	10	9	6	3	4		1	2				52	12.2
pumilum				1	4	6	7	12	9	9	5	6	6	3		1	69	17.4
creticum	2	3	8		3		1				1						18	6.2

Table 18

Length of rays in terminal umbel (mm) mean per umbel. Variation between some collections of different species. Spontaneous material.

The means given have been calculated from the exact measurements, and not from those shown here.

Species	Coll. nr.	12	14	16	18	20	22	24	26	28	30	32	34	36	38	40	n	M
cynapioides	E44				3	3	3	1	2								12	22.3
tuberosum	E52			1	1	6		6	3	1	2						20	24.2
	E53					2		1	1	4	3	5	3			1	20	30.5
capillifolium, 2n=10	E45		1	2	5	3		2	2								15	19.0
	E46			1	5	4	1	2	1								14	19.2
	E47				2	3		3	3	1		1					13	22.5
	E51					1	1	8	5	3	1	1					20	24.6
capillifolium, 2n=20	E49			2		7	2	1	4	3		1					20	21.9
stylosum	E66		3	2	6	9	6	9	7	2	4	1	1				50	21.7
	E67		1	6	7	11	12	5	4	3	1						[illegible]	[illegible]

developed, usually have more rays than the terminal one.

As seen from Table 20 there is often a wide range of variation within populations. In collection E44 (G. cynapioides) the number of rays varies from 5 to 13 although the mean is the same as for all material of the species seen. (Table 19). The situation is almost the same in the collections E52 and E53 (G. tuberosum). In G. capillifolium the tetraploid collection E49 differs from the diploids in having a higher mean. However, the number of rays varies from 6 to 12 without any conspicuous mode, and the total range is the same as in collection E45. The difference found between the two collections of G. stylosum is statistically significant.

In Table 19 all material seen is presented. G. bornmuelleri is outstanding with a mean of 13.3 rays and a range from 11 to 15. There is some overlapping with the erect species G. cynapioides, G. tuberosum and G. capillifolium, but these species have means around 8 and a total distribution from 3 to 14. The mean of the first two species is more than 8 and for the last one 7.7. The difference is statistically significant but in this respect tetraploid G. cappillifolium more closely resembles G. cynapioides and G. tuberosum.

In the pumilum-pindicola complex G. pindicola is well separated with a mean of 4.8 while the other species have about 3 rays. In G. pumilum the number three is dominant giving most plants a very typical appearance.

The number of rays seems to be little influenced by environmental conditions. Material from most of the populations in Table 20 has been tested in cultivation. Except in the collections of G. stylosum there are only small alterations in the means and the ranges of variation (Table 22). The means of E66 and E67 have increased from 6.5 to 8.1 and 5.4 to 6.9 respectively.

In several species it has been noted that the number of rays can change from one year to another in the same individual.

Table 19.
Number of rays in terminal umbel. All spontaneous material seen.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	n	M
macrocarpum			3	4	13	12	8	6		1						47	5.9
stylosum				1	41	41	22	15	3							123	6.1
bornmuelleri											3	1	4	3	4	15	13.3
pumilum	1	9	34	7		2										53	3.0
peloponesiacum		4	12	6	1	1										24	3.3
creticum		5	3	1	1											10	2.8
pindicola		2	9	38	39	17	10									115	4.8
cynapioides				1	1	3	5	14	7	4	2		1			38	8.2
tuberosum					3	18	26	38	30	18	10	2	3	3		151	8.4
capillifolium			1	3	19	47	49	59	43	19	9	5	1			255	7.7
parnassicum			1	20	37	18	6	3		1						86	5.3
euboicum				3	3	1	1									8	5.0

Table 20.
Number of rays in terminal umbel. Variation between some collections of different species.

Species	Coll. nr.	4	5	6	7	8	9	10	11	12	13	14	n	M
cynapioides	E44		1		3	5	1	1			1		12	8.2
tuberosum	E52			1	2	10	4	2				1	20	8.5
	E53			2	1	8	4	4	1				20	8.5
capillifolium, 2n=10	E45			5	3	5		1		1			15	7.5
	E46			2	2	6	4						14	7.9
	E47			1	2	6	4						13	8.0
	E51		2	9	8	1							20	6.4
capillifolium, 2n=20	E49			3	4	2	6	1	3	1			20	8.6
stylosum	E66		4	24	14	7	1						50	6.5
	E67	1	32	15	2								50	5.4

NUMBER OF FLOWERS AND THE POTENTIAL CAPACITY OF SEED PRODUCTION

The number of flowers was estimated in some populations by counting one umbellet selected at random in each terminal umbel.

The intrapopulational variation is great but there are considerable differences between species. The populations of G. tuberosum and G. cynapioides investigated are, however, very similar with means from 13.5 to 15.8. E52 ranges from 7 to 18 flowers without a distinct mode, which perhaps is due to the limited material. The Adriatic group is well separated from G. capillifoliu in the number of flowers. The latter species is represented by 4 populations and the greatest difference between means is 0.7. Even the tetraploid lies within these limits. G. stylosum has about 11 flowers the number ranging from 7 to 15.

The percentage of hermaphrodite flowers was calculated in the umbellet. The intrapopulational variation is considerable but the means are about 30--60% in most populations (Table 22).

Collection E44 (G. cynapioides) is exceptional in that more than 90% of the flowers are hermaphrodite. Collection E46 (G. capillifolium) has the lowest value which is about 30%.

With the help of the percentages of hermaphrodite flowers, the number of flowers in the umbellet and the number of umbellets in the terminal umbel one can get an estimation of the potential capacity of reproduction (Table 22).

Plants of collection E44 (G. cynapioides) produce about 110 fruits in the terminal umbel which is twice as many as the plants of collections E52 and E53 (G. tuberosum). Tetraploid G. capillifolium produce up to 84 fruits while the diploids produce only from 40 to 60. The two collections of G. stylosum, E66 and E67, can produce 46 and 24 fruits respectively.

These considerable differences in reproductive capacity could theoretically be compensated for by the production of secondary umbels. However, Table 13 shows the opposite to be true. Generally populations which produce few fruits

Table 21

Number of lowers in an umbellet of the terminal umbel. The umbellet was selected at random. Spontaneous material.

Species	Coll. nr.	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	n	M
cynapioides	E44						2	1	2	3	1	1						10	14.3
tuberosum	E52	1			2		3	3	4	3	3		1					20	13.5
	E53							1	3	4	7	4			1			20	15.8
capillifolium, 2n=10	E46									1	5	3	1	3		1		14	17.4
	E47							1		2	1	2	3	3	1			13	17.2
	E51									1	3	3	6	5	1	1		20	17.9
capillifolium, 2n=20	E49							3	1	2	2	2	4	1	2	2	1	20	17.2
stylosum	E66		1	1	2	7	4	2	2	1								20	11.6
	E67	1		2	4	4	6	3										20	11.0

Table 22

Potential capacity of seed production by terminal umbel. Spontaneous and cultivated material.

Species	Coll. nr.	Number of rays		Number of flowers/ umbellet		Percentage of herma-phrodite flowers		Number of fruit/ terminal umbel	
		spont.	cult.	spont.	cult.	spont.	cult.	spont.	cult.
cynapioides	E44	8.2		14.3		93.0		109	
tuberosum	E52	8.5	8.0	13.5	13.8	48.1	44.4	55	49
	E53	8.5	8.3	15.8	15.8	41.0	39.7	55	52
capillifolium, 2n=10	E46	7.9	7.4	17.4	16.3	30.3	48.0	42	58
	E47	8.0	8.5	17.2		42.9		59	
	E51	6.4	6.2	17.9	17.9	39.7	40.3	45	45
capillifolium, 2n=20	E49	8.6	9.1	17.2	17.2	57.0	44.3	84	69
stylosum	E66	6.5	8.1	11.6	11.4	60.6	70.1	46	65
	E67	5.4	6.9	11.0	10.5	40.5	49.1	24	36

also produce few branches. Furthermore it has been noted that fruits are oftener developed on secondary umbels in the many-branched species. Consequently the differences in reproductive capacity are much greater than is shown in Table 22.

As seen in Table 22 the number of flowers remains almost unchanged in cultivation. Only in collection E46 does the mean show a decrease from 17.4 to 16.3.

The percentages of hermaphrodite flowers are more easily influenced by environmental factors. For collection E46 this value has increased by 18% while for E49 it has decreased by 13%. In both the populations of G. stylosum examined the value has increased by about 10%.

Thus the number of rays and the number of flowers hardly change while the ratio of hermaphrodite flowers may change in both directions under different conditions. Nethertheless the wild material demonstrates that in nature there are great differences in reproductive capacity, at least this was so the year the material was collected.

G. cynapioides needs a higher reproductive capacity than G. stylosum in order to keep the size of the population unchanged. Thus in G. cynapioides either seedling establishment is less successful or else the plants are less long-lived. There is no indication that G. cynapioides and tetraploid G. capillifolium are shorter-lived (see Size of tuber) than other species.

LENGTH OF PEDICELS

The length of the pedicels is a character separating G. pindicola and the species of the pumilum group. The measurements presented in Fig. 32 are made on wild material with ripe fruits.

Overlapping occurs between almost all populations but the intrapopulational variation is fairly uniform with a distinct mode close to the mean.

G. pindicola has the longest pedicels. Of the three populations shown in

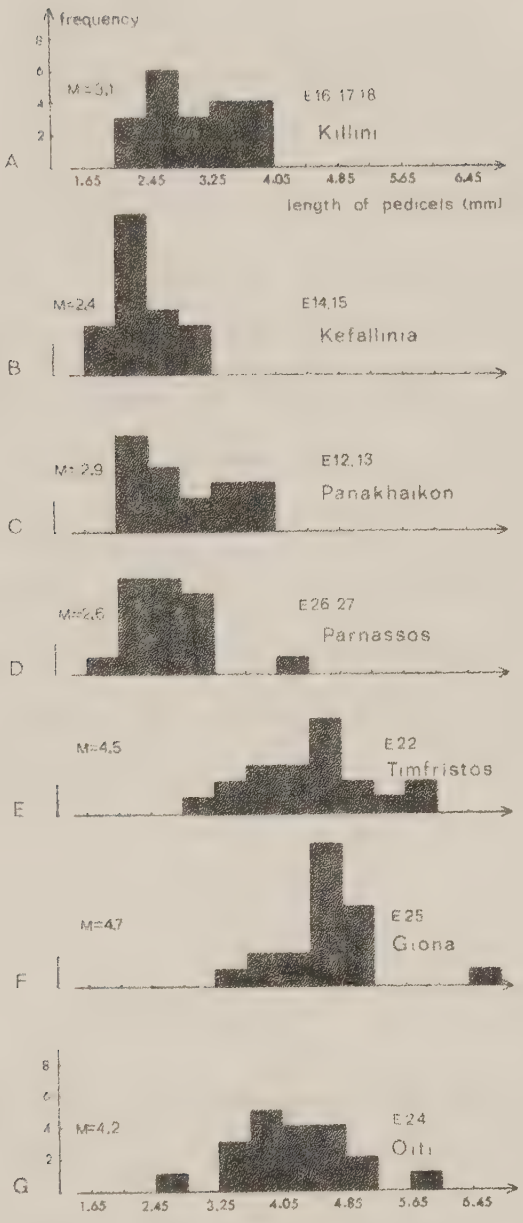


Fig. 32. Length of pedicels (mm) in some populations of the pumilum--pindicola-complex. -- A--C: G. peloponesiacum. -- D: G. pumilum. -- E--G: G. pindicola.

Fig. 32 that from Mt Oiti has the shortest pedicels with a mean of 4.2 mm. Four individuals available from Mt Peristeri have a mean of 3.7 mm, but there is still a clear distinction between G. pindicola and the species of the pumilum group. The three plants of G. creticum have a mean of 2.3 mm which is the lowest in the complex. In the three populations of G. peloponesiacum investigated the means vary from 2.4 to 3.1 mm. In G. pumilum the corresponding value is 2.6. Thus the three species of the pumilum group cannot be separated from one another on the pedicel length, but the group is distinct from G. pindicola.

The length of the pedicels has also been measured in populations of other species but on very limited material. The means are:

G. macrocarpum: E1 Naxos 4.7, E4 Tinos 3.5, E7 Mt Imittos 3.2, E8 Rodhos 4.3, E10 Pelagos 5.9. As seen there is considerable interpopulational variation in this species, G. capillifolium: E11 Mt Athos 5.8, E23 Mt Oiti 3.8. G. parnassicum: E5 Mt Parnis 3.4. G. euboicum E9 4.4.

DIAMETER OF PEDICELS

The diameter of the pedicels was measured on the same material as the length.

The type of variation is the same as for the length of the pedicels and the pumilum group can also be separated from G. pindicola on pedicel diameter. The means for G. creticum and G. pumilum are 0.36 and 0.37 mm respectively. Material of G. peloponesiacum from Panakhaikon and Killini are pedicels 0.33 mm thick while in that from Kefallinia they are 0.36 mm thick ones. In the populations of G. peloponesiacum examined the values vary from 0.28 to 0.32.

The lowest value found in a tetraploid species is 0.28 mm and the highest value in a diploid species is 0.21. In G. euboicum (chromosome number not known) the diameter of the pedicels was found to be 0.28 mm, which suggests that the species is tetraploid.

FRUIT

The size of the fruit is related to the chromosome number. In diploid plants the fruits are about 4 mm long or less (style and stylopodium excluded), species with higher chromosome numbers having fruits about 5 mm long or more. Variation in the length of the style and stylopodium is irregular. The longest are found in some Turkish populations of G. stylosum and in G. creticum, both about 1.7 mm In the Samos population of G. stylosum the style and stylopodium are only about 1.4 mm long, in G. capillifolium about 1.0 mm or less independent of chromosome number, and in G. tuberosum and G. cynapioides 1.3 mm or more. The shape of the dry stylopodium is mentioned under the taxonomy. The collar is most prominent in the species of the Aegean group but there is some variation. The most conspicuous collar is found in Mt Imittos, Tinos and Naxos material of G. macrocarpum while in the Rodhos material it is rather small and similar to that of most other species.

Examples of intra- and interpopulational variation of the shape of the mericarps are presented in Fig. 33. A--F show representatives of G. capillifolium. Independent of chromosome number the mericarps are recognized by the dorsal ridges which are curved from the top to the lower part. The other species presented in Fig. 33 are recognized by a fairly long sterile part at the apex and a dorsal ridge which is slightly curved or not in the middle. Mericarps of G. euboicum are recognized by the abruptly bent styles and the sterile part which often is bent inwards. In spite of these general characteristics some inter- and intrapopulational variation is found in both the size and the shape of the mericarps.

THE TOOTHED FRUIT RIDGES OF G. PUMILUM

In G. pumilum the ridges of the fruits sometimes have minute teeth or smaller

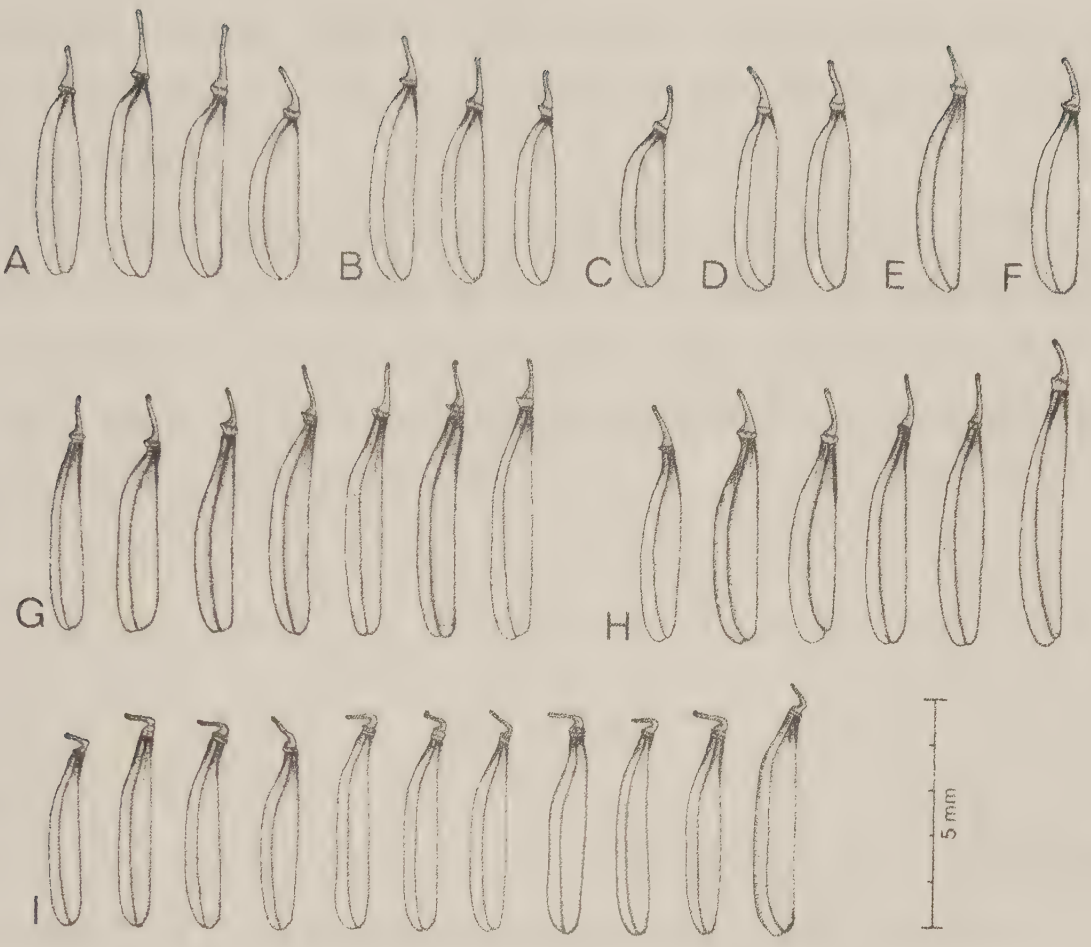


Fig. 33. Intra- and interpopulational variation of mericarps. -- A--F: G. capillifolium. -- A: E45, Gargano, Italy. -- B: E46, Ipsiz Oros, Greece. -- C: E47, Ipsiz Oros, Greece. -- D: E51, Mt. Lovcen, Jugoslavia. -- E: E11, Hagion Oros, Greece. -- F: E49, Cakor, Jugoslavia (2n=20). -- G: G. macrocarpum. E8, Rhodos. -- H: G. peloponesiacum. E12, E13, Mt. Panakhaikon, Greece. -- I: G. euboicum. E9, Euboea, Greece.

more rounded tubercles. (See III Taxonomy). This character has proved to be connected with the pubescence of the peduncles. Table 23 shows the relationship in 62 individuals.

Of the 29 individuals which are considered to have prominent teeth (difficulties arise due to differences in degree of maturity), 24 had hairy peduncles. In 33 individuals teeth were small or absent, 30 of them being glabrous.

This is one of the few examples of intrapopulational polymorphism in qualitative characters found in the genus.

BRACTLETS

Number of bractlets

The shape of the bractlets is a traditional character used in the taxonomy of Geocaryum but the number has also proved to be of some importance.

The number of bractlets is presented in Tables 24 and 25. As umbellets may differ within an umbel an individual has been represented by the maximum number found in an umbellet of the terminal umbel.

Table 24 presents all material seen of all species except G. divaricatum. The pumilum-pindicola complex differs from the rest of the material, the maximum number being 5 but with means of between 3.1 and 3.6. No other species has a mean below 5.0. It has been found that a tall individual withmany branches and primary rays also has the highest number of bractlets and this is true of G. pindicola, which is often more "viable" than the rest of the complex. The same tendency is found in the Aegean group. G. macrocarpum and G. stylosum are very constant, both with means of about 5. G. bornmuelleri has a mean of 5.4 and is in all respects larger than the other two. The limited variation found in G. macrocarpum does not only apply to the species as a whole but also to individual umbellets.

Table 23. G. pumilum.

Correlation between toothed fruit ridges and hairy peduncles. Spontaneous material.

	Prominent teeth	Teeth small or absent	Total
Peduncle glabrous	5	30	35
Peduncle hairy	24	3	27
Total	29	33	62

Table 24.

Number of bractlets. Each individual represented by that umbellet of the terminal umbel which has the highest number of bractlets. All spontaneous material seen.

Species	1	2	3	4	5	6	7	8	9	n	M
macrocarpum				1	43	1				45	5.0
stylosum				4	104	12	1	1		122	5.1
bornmuelleri					9	6				15	5.4
pumilum	1	7	42	18						68	3.1
peloponesiacum		7	30	15	3					55	3.3
creticum		1	13	4						18	3.2
pindicola		6	37	37	10					90	3.6
cynapioides					1	10	23	2		36	6.7
tuberosum			12	25	51	45	13	1	1	148	5.2
capillifolium (tot.)				3	49	89	61	24	4	230	6.3
capillifolium, Italy					1	12	15	10	3	41	7.0
capillifolium, Balkan				3	48	77	46	14	1	189	6.1
parnassicum			3	9	22	11	2			47	5.0
euboicum				1	6		1			8	5.1

Table 25.

Number of bractlets. The highest number found in an umbellet of the terminal umbel. Variation between some collections of different species. Spontaneous material.

Species	Coll. nr.	4	5	6	7	8	9	n	M
cynapioides	E44			6	6			12	6.5
tuberosum	E52	3	7	9	1			20	5.4
	E53		2	12	6			20	6.2
capillifolium, 2n=10	E45			5	5	3	2	15	7.1
	E46		1	7	4	1	1	14	6.5
	E47		1	6	6			13	6.4
	E51		5	8	6	1		20	6.2
capillifolium, 2n=20	E49		2	7	9	1		19	6.4
stylosum	E66	2	39	7	1	1		50	5.2
	E67	2	44	4				50	5.0

There is a significant difference in the number of bractlets between the Adriatic species G. tuberosum and G. cynapioides. However, the ranges of variation overlap. G. tuberosum has thewidest variation which is probably not only because of the greater material studied. The means of the two collections E52 and E53 (G. tuberosum) differ considerably. (Table 25).

In G. capillifolium as well the wide range of variation in other characters is accompanied by wide variation in the number of bractlets. Collection E45 from Gargano, Italy, differs from the other collections. In Table 24 G. capillifolium has been divided up into Italien and Balkan material. There is a significant difference between these two groups, the mean of the Italian material being 7.0 and of the Balkan material 6.1, the same tendency being found in the Italian G. cynapioides and the Balkan G. tuberosum.

G. parnassicum has a mean of 5.0 but displays great interpopulational variation compared with G. macrocarpum. G. euboicum falls inside the range of G. parnassicum.

In Table 26 is presented the distribution of bractlets in localities of G. peloponesiacum. In spite of the limited material the similarities are noticeable. Only material from Taiyetos differs but the range of variation is the same.

Shape of bractlets

In species with the chromosome numbers 2n=18 and 2n=20 bractlets are generally lanceolate or ovate in outline, those of the diploids being more or less linear. G. parnassicum shows great variation in this respect with a ratio length/width varying between 3 and 7. Another exception is G. stylosum where the ratio can be up to almost 10. The bractlets of G. cynapioides are more or less lanceolate basal part which often has a long setose point, those of G. capillifolium are linear independent of ploidy level.

Table 26.

Number of bractlets in G. peloponesiacum. Herbarium material representing different collections from the mountains.

Mountain	2	3	4	5	n	M
Panakhaikon	2	8	6	1	17	3.4
Kefallinia	1	2	0	1	4	3.3
Taiytos	3	5	0	1	9	2.9
Killini	0	11	16	0	17	3.4
Aroania	1	4	3	0	8	3.3

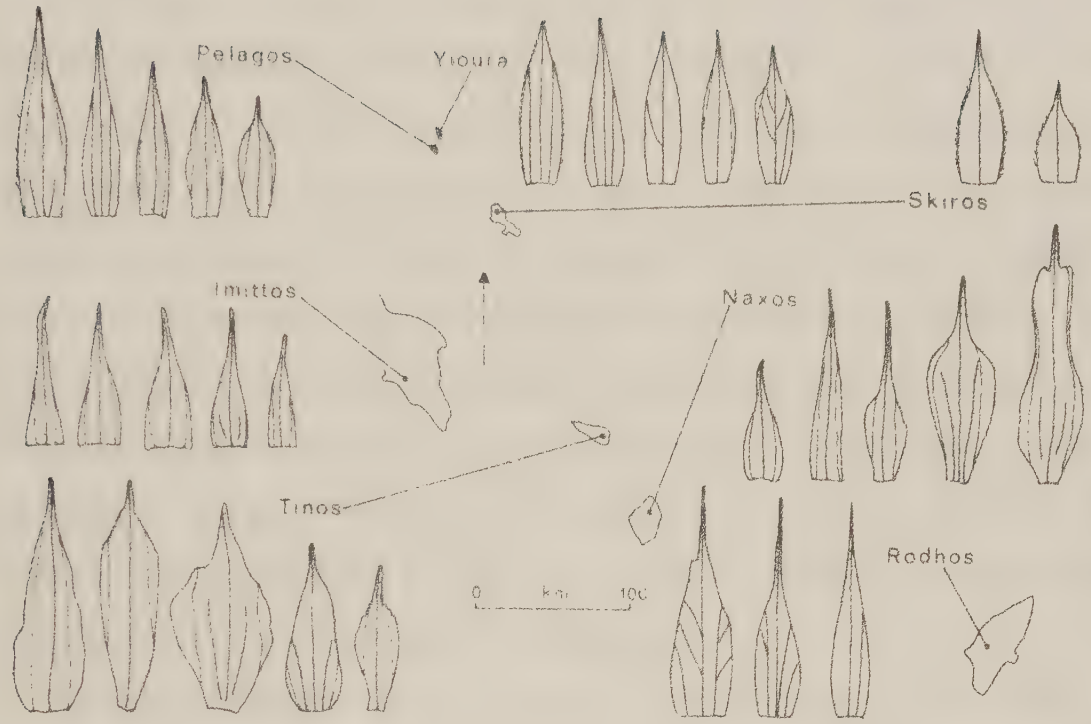


Fig. 34. Variation in shape and size of bractlets in some populations of G. macrocarpum. The bractlets are from different individuals. -- Drawings X5.8.

At least in the periferal part of the umbel the bractlets which point outwards are longer than those which point towards the centre of the umbel so that the size of bractlets is usually a poor distinguishing character.

The shape of bractlets varies only slightly within populations but the intrapopulational variation is generally considerable. An example from G. macrocarpum is given in Fig. 34. Material from Skiros is recognized by its ovate shape and by being shortly ciliate. Ciliate bractlets may also occur in plants from Yioura and Pelagos but they are lanceolate and often with a membraneous margin. Bractlets from Mt Imittos are narrowly triangular and always have a membraneous margin although it can sometimes be narrow. Material from Naxos and Tinos is irregular in shape. The demonstrated range of variation can be found in a single individual. Bractlets from the Rhodos material have no membraneous margin and have a long, almost setose point, a character which connects it with Turkish material of G. macrocarpum.

A variation pattern such as that of G. macrocarpum is also found in the widespread species G. capillifolium and G. tuberosum. The total variation in G. pindicola and G. parnassicum is even greater.

SIZE OF POLLEN GRAINS IN G. CAPILLIFOLIUM

The morphology and size of pollen grains is described in II. Morphology and general description. There are significant differences in size between grains of plants with the somatic chromosome numbers 10 and 18 or 20.

The taxonomic difficulties with some material of G. capillifolium especially from the surroundings of Nis in Serbia are mentioned in III. Taxonomy. As it not has been possible to get living material from this area the chromosome number is not known. In morphology, herbarium material shows similarities with both known diploids and known tetraploids.

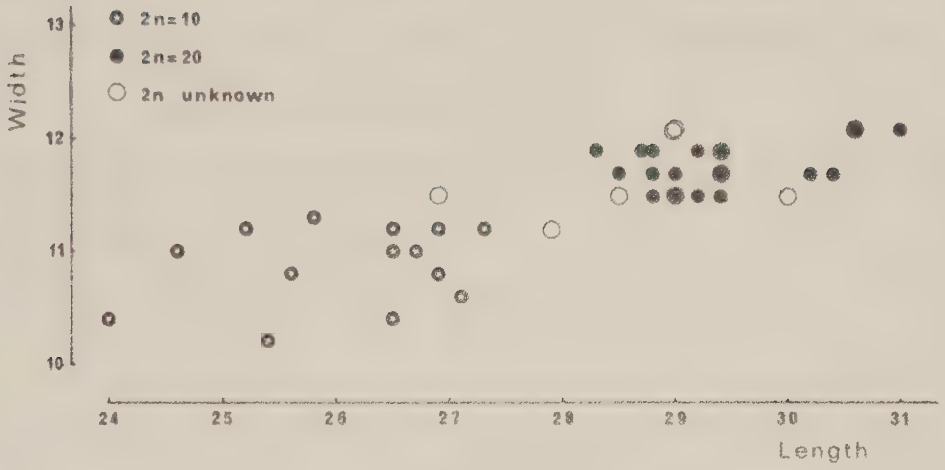


Fig. 35. Diagram showing length and width (µm) of pollen grains of G. capillifolium. Each mark represents the mean value of ten grains per individual. -- Stardots: Known diploids from the collections E45, E46, E51. -- Dots: Known tetraploids from the collection E49. -- Rings: Ten different collections from the surroundings of Nis, Serbia.

Length and width of pollen grains of 14 diploids with known chromosome numbers (E45, E46, E51) and 17 tetraploids (E49) are shown in Fig. 35. In the same diagram measurements of 10 herbarium sheets collected in Serbia close to Nis are plotted. All measurements have been made on dry material. Each symbol represents mean value of 10 grains per individual.

Of the 10 herbarium sheets investigated 8 fall entirely inside the cluster of tetraploids. Two individuals have an intermediate position. These were collected in the alpine zone of Mt Midzor E of Nis and in the montane zone of Mt Selischewitza S of Nis. Both zones are represented by other collections which fall inside the tetraploid cluster.

According to the measurements of pollen grains the Serbian material of G. capillifolium is tetraploid.

PATTERN OF VARIATION AND DIFFERENTIATION

(1) The intrapopulational variation in a single character may be wide compared with the total variation of the species, which may partly arise from the fact that only a few populations of most species have been studied. The intrapopulational variation of a quantitative character is usually continuous, but most populations can be distinguished from one another on a combination of qualitative or quantitative characters.

(2) Several characters show an irregular occurrence in the genus, among which have been mentioned chemical components, the toothed pedicels, size of fruits and length of leaf lobes. Others are the recurved styles which occur in G. euboicum and in the Mt Imittos and Mt Parnis populations of G. macrocarpum and the length of the style and stylopodium. This type of variation has caused most of the taxonomic difficulties in the genus.

(3) Some of the total variation in the genus is connected with differences in chromosome numbers, however not between species with 2n=18 and 2n=20. The characteristics of diploid plants are: smaller tubers, a slender habit, long and narrow bractlets, long and narrow leaf lobes, smaller fruits, smaller pollen grains. Of these the size of the pollen grains is, as expected, the most reliable and this is also one of the few safe characters that distinguish diploid from tetraploid G. capillifolium.

(4) Of the characters used to divide the genus into subgroups some are constant others vary. The anthers are always dark red in the G. pumilum group but never in other species. In the Aegean group the anthers are either pink or greenish-white. The colour of the stylopodia is constant within each group. The shape of the dry stylopodium, the collar, may change and there is some overlapping. The toothed pedicels are an unreliable character.

(5) There are few examples of intrapopulational polymorphism, characters which tend to be established in, or removed from populations. The chromatographic work is very useful for a study of this phenomenon. The toothed fruit ridges in G. pumilum is another example.

(6) It is difficult to make suppositions about the selective value of characters. Some of the variation may be haphazard but most of it is probably adaptive. The colour of the anthers and stylopodia can be of importance for pollination because it influences the vizual impression of the umbel. This is also true of variation in number, shape, and colour of the bractlets even if the effect not is so strong in Geocaryum as in Astrantia and Chaerophyllum creticum.

The hooked styles and also the toothed fruit ridges can be of value in the distribution of the mericarps.

The different stem habits are well adapted to different habitats. The incision of the leaves and the shape of the leaf lobes is more difficult to inter-

pret. However, in the mainly Iberian genus Conopodium there is an almost identical type of differentiation in the shape of the leaf lobes, which is accompanied by similar types of stems and similar types of environment. It has been noted that other umbelliferous plants growing together with Geocaryum species often have a similar type of leaf lobes. Examples are Bunium alpinum ssp. montanum which grows together with G. tuberosum, and Pimpinella serbica which grows together with tetraploid G. capillifolium. In particular the parallel differentiation with Conopodium indicates that the type of leaf incision is adapted to special habitats.

(7) The phenotypes studied have proved to be almost entirely unmodified in cultivation. Some small differences were noted in the vegetative development, mainly in the length of the stem.

VII. DISCUSSION

SOME CONCLUSIONS FROM THE PREVIOUS PAGES

(1) All species are mainly self-pollinated. There is a mechanism which promotes selt-fertilization.

(2) It is possible to produce hybrids in only a few conbinations.

(3) Male fertility is very high.

(4) Cytologically deviating individuals are rare in populations.

(5) Diploidy, tetraploidy and aneuploidy occur in the genus.

(6) The intrapopulational variation is continuous.

(7) Irregular occurrence of characters makes the taxonomy difficult.

(8) Populations vary in size from 10--50 individuals to hundreds of thousands.

(9) The populations are geographically isolated from one another.

(10) The species are confined to very specific habitats.

(11) There are no surprising gaps in the phytogeographical distribution.

(12) Vegetative propagation does not occur.

(13) All species are geophytes.

ORIGIN, MIGRATION AND PHYTOGEOGRAPHY

Within a circle whose centre is just SE of the city of Levadhia (Voiota, Greece) and with a radius of less than 100 km, 8 of the 13 species occur. This southern part of Greece is the centre of diversity. The area within the circle includes the diploid species G. parnassicum and the most southern locality for G. capillifolium and it also includes representatives for the pumilum-pindicola complex, the Aegean group and the two dubious species G. euboicum and G. divaricatum.

Tetraploidization of an ancestral diploid form has probably taken place in this area. At present it seems impossible to decide whether the process of tetraploidization is mono- or polyphyletic. The result was, however, three lines of differentiation (too little is known about G. euboicum and G. divaricatum to make any speculations about them).

The first line was distributed mainly eastwards and inhabitated the former area of land of the present Aegean area. In the south it was stopped by the south Aegean Sea which prevented it from reaching present-day Crete. In the southeast the Turkish mainland was connected with Rodhos. In the north it reached at least as far as the present island of Thasos. This line gave rise to the Aegean group (G. macrocarpum, G. stylosum, G. bornmuelleri). G. bornmuelleri is endemic to the island of Thasos in the northern Aegean Sea. G. stylosum grows in a rather limited area in W Turkey and on the island of Samos.

As pointed out by Rechinger (1943, 1947, 1950, 1951) there is a strong phytogeographical boundary between the Cyclades and the E Aegean islands, which indicates a break of considerable antiquity in the Aegean land area (Rechinger 1951 , Wettstein 1953, Creutzburg 1963). Several other authors have discussed the phytogeography and the geological history of the C and S Aegean, e.g. Snogerup 1967 b, Runemark 1969, Greuter 1970, 1971, and Strid 1970. There is no disagrement about the fact that floristically Samos belongs to Asia Minor.

G. macrocarpum is distributed on several islands of the Northern Sporades,

southern Attiki, the Cyclades islands Andros, Tinos, Naxos, S and W Turkey and Rodhos. The species thus crosses the phytogeographical boundaries of the C and S Aegean. The land-bridge which connected Greece with Asia Minor is presumed to have started to break up in the mid-Pliocene, i.e. about 5 million years ago. Rodhos and S Turkey became definitely isolated from the Cyclades. An arm of the sea also penetrated from the south isolating the Cyclades from the Greek mainland. They were, however, brought in contact again during the Pleistocene (Wettstein 1953). Rodhos must have become isolated earlier than Samos. The species G. macrocarpum must thus be more than 5 million years old.

According to Runemark (1969) forests of Quercus coccifera have played an important part in the vegetation of the C Aegean. Closed forests are now almost non-existent. Forests either consisting of Quercus coccifera or Pinus and Cupressus as on Rodhos may have been the original habitats for G. macrocarpum. G. macrocarpum is a Tertiary relict which has managed to survive in some localities due to special ecological conditions. In the Cyclades and the Northern Sporades the best substitute for Quercus forests is shrubs of for instance Pistacia and Arbutus or, as on Tinos, phrygana. The water conditions are probably of greatest importance. The dominating moist northernwinds cause a certain amount of dew to form on the highest areas of the islands Andros, Tinos, and Naxos. In the Northern Sporades the water conditions are slightly better than in the Cyclades and a poor macchia vegetation, which forms a suitable habitat for G. macrocarpum is found at lower altitudes.

The fragmentation of the Cycladian block was not a continuous process owing to subsequent glacial periods causing regressions of the sea followed by transgressions during interglacials.

In G. macrocarpum it is possible to trace a regional differentiation. The Cycladian populations have in common the general habit, shape of fruits and shape of bractlets (see Fig. 34). The two mainland populations on Attiki are recognized by the curved styles. The two populations from Rodhos are similar

especially as regards the pointed bractlets. The regional differentiation stresses the phytogeographical division of the C and S Aegean.

The second line which should have derived from tetraploidization spread southwards and gave rise to the pumilum group. G. pumilum is endemic to Mt Parnassos N of the Gulf of Corinth. G. peloponesiacum is spread over Peloponnisos and on the island of Kefallinia while G. creticum is endemic to Crete.

The mountains of Crete formed part of a land-bridge which connected Peloponnisos with Asia Minor during mid-Tertiary times (Greuter 1971). According to Greuter (1972) the isolation of Crete began in the upper Miocene, i.e. about 10 million years ago. The Gulf of Corinth existed during the late Pliocene but Peloponnisos and the mainland were again connected during the glacial periods of the early Pleistocene (Creutzburg 1963).

The geographical isolation of G. creticum is presumably about 10 million years old but the biological isolation could have started long before the break--up of the land-bridge. On the other hand, the strait may have been narrow enough during the Pleistocene glacials to have permitted the immigration of plants.

The distribution on Crete is uncertain. Material has been seen from the Lasithi area only. If this is the only place where the species grows it should be included among the "stenendemiten" (Greuter 1971). However there is a note in the literature about its presence on Idhi Oros as well which seems plausible for a Tertiary relict which has invaded Crete from the west.

G. peloponesiacum grows on the highest mountains of Peloponnisos and on the island of Kefallinia. The island population grows in a stony open Abies cephalonica forest, while the others are found above the tree limit on screes and stony slopes. It seems possible that open forests were the original habitats for the species but that increased competition from other plants has forced the Peloponnisos populations to emigrate to higher altitudes. In the mobile screes the competition is very limited. They are inhabited by five to ten species and

most of the ground is bare. The increase in competition in Abies forests could have been caused by climatic changes during the Pleistocene. The relatively unchanged conditions on Kefallinia can either be the result of isolation which prevented more aggressive species from invading or ecological conditions.

Morphological features indicate that G. pumilum and G. peloponesiacum are very closely related while G. creticum is somewhat further removed.

The third tetraploid line gave rise to G. pindicola. It spread to the northwest and occupied mountains of the Greek mainland, mainly the Pindhos Mts. In morphology and ecology it is similar to the pumilum group and it seems possible that the two lines originated from a common tetraploid form. Recent investigations in the Pindhos Mts. (Aldén, Gustavsson unpubl.) have shown that G. pindicola is common in the montane and alpine areas.

The diploid species G. parnassica is mainly distributed on Peloponnisos and is also found in a few localities on the Greek mainland. According to J. Persson (pers. comm.) the species is found in more sheltered and moister places than G. peloponesiacum inhabits, for instance at the base of cliffs or slopes or in the upper parts of dry Abies cephalonica forests. The species from Peloponnisos have never been found together in the same localities but often inhabit the same mountain areas. It is obvious that they grow in different habitats. From Mt Parnis (Attiki) there are some collections in which G. parnassicum is mixed with G. macrocarpum.

The southermost locality where diploid G. capillifolium is found is on Mt Oiti (Phtiotis) in an Abies forest where conditions are more favourable than on those of Peloponnisos. The flora here is considerably richer in herbs and grasses. On Mt Timfristos the forest is sometimes dominated by Pteridium. Further north Abies cephalonica is replaced by Fagus silvatica and also by Quercus or other deciduous trees.

G. capillifolium is often found growing in the same mountains as G. pindicola but in more sheltered localities and usually at lower altitudes. In Greece

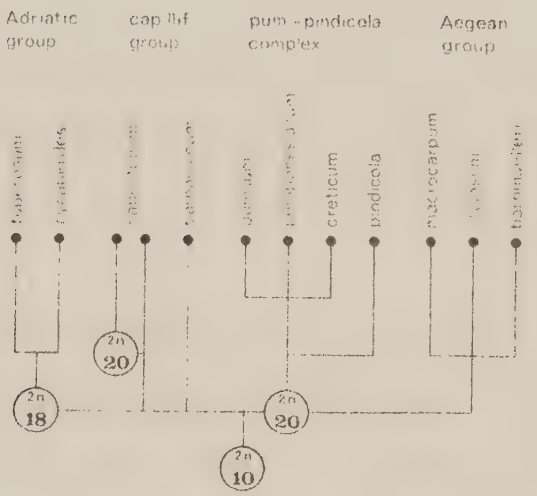


Fig. 36. Putative phylogenetic relationship between the species of Geocaryum (G. divaricatum and G. euboicum excluded).

G. pindicola and G. capillifolium are vicarious with G. peloponesiacum and G. parnassicum on Peloponnisos.

G. capillifolium seems to have originated as an ecotype adapted to the special environmental conditions in the northern Abies cephalonica forest. This form is called type (3) in the taxonomic part. The species has managed to spread further north and occupy the deciduous forest where type (2) of G. capillifolium has developed.

G. capillifolium has been successful. In the Balkan Peninsula the diploid cytotype is now distributed from Mt Athos and Khakidhiki in the east to the Adriatic Sea in the west. In Italy it occurs on Mt Gargano, in Lucania and on Sicily.

There is a close connection between the flora of S Italy and that of Dalmatia. Turrill (1929) listed more than a hundred species which he regarded to be endemic limited to Italy and the Balkan Peninsula.

On the Balkan Peninsula G. capillifolium has given rise to a tetraploid form which has invaded montane and alpine meadows. In the inland of the peninsula it is distributed northwards to the surroundings of Nis in Serbia and the adjacent part of Bulgaria. Thus the tetraploid seems to be more tolerant to the inland conditions and also to higher altitudes, at least in the central part of the peninsula.

The aneuploid species, G. tuberosum and G. cynapioides, have presumably originated from the same ancestral stock as G. capillifolium. With the facts known at present it is not possible to say whether the species have derived from diploid or tetraploid forms, nor it is possible to say whether they are of monophyletic or diphyletic origin. Fig. 36 shows probable phytogenetic relationships between the species of Geocaryum (G. divaricatum and G. euboicum excluded).

MODES OF EVOLUTION

The formation of tetraploids and aneuploids has been a major advance in the evolution of Geocaryum. Tetraploidization has apparently taken place at least twice, giving rise to the tetraploid form of G. capillifolium and then to the species of the Aegean group and those of the pumilum-pindicola complex. In G. capillifolium the tetraploidization has not led to any pronounced morphological changes and to some extent this is also true of the other tetraploid groups. However, the two cytotypes of G. capillifolium have different habitats, the tetraploids generally growing at higher altitudes than the diploids a fact which has made it possible for the genus to expand its distribution to new and more inhospitable areas.

This case could be compared to the situation in arctic regions, where most of the species are polyploids. It has been assumed that the increased genetic variability has made it possible for them to occupy new areas (for a discussion see Böcher 1972), though increased genetic variability is not in itself a reason for occupying inhospitable areas. The primary reason is more likely to be competition from the diploid forms which are already well adapted to the special biotype, thus forcing the poyploids to occupy new areas which are not inhabitated by plants with similar ecological demands.

Migration to new biotopes must have been accompanied by adaptation through selection. At this stage the genetic variability achieved by tetraploidization must have been useful.

The result of the adaptive radiation can be traced in for instance the differences between the Aegean group and the pumilum-pindicola complex. In the Aegean group in particular the species differ from one another and seem to be well adapted to different biotopes. Another case of adaptative radiation is the origin of G. capillifolium and G. parnassicum as ecotypes from a probable common ancestral form.

Thus adaption through selection has played an important part in the evolu-

tion of the species but it cannot explain all the variation found in the species or between the species of the pumilum-pindicola complex, for example. Most populations of these groups grow under similar conditions. The type of variation found can be described as vicariance in the sense of Bramwell (1972).

At present the isolation of populations of different mountains or islands is absolute. Populations in different localities on the same mountain may also be completely isolated. The size of populations varies from 10--50 individuals up to hundreds of thousands. The species of the pumilum-pindicola complex in particular are recognized by rather small populations while those of the northern erect species are more numerous. Geographical isolation and small populations are factors that stimulate the process of vicariance which arises from an interaction of genetic drift and selection. Thus the characters established by vicariance do not always have an adaptive value.

It has been shown that it is possible to produce hybrids even between species. However, most of the crossing experiments have failed and in nature the geographical isolation is absolute. In no case has hybridization been found to have contributed to the evolution of the genus.

The biological circumstances in Geocaryum do not support rapid evolution. Hardly any cytologically deviating individuals are found in the populations, male fertility is high, self-pollination should have caused a high degree of homozygotization and Geocaryum today displays genetic stability. Greuter (1972) has discussed non-evolution in relict taxa but the term non-evolution seems to be too strong to apply to Geocaryum. The species are of great age but considerable interpopulational differentiation has taken place since the formation of the species.

THREATENED SPECIES

Geocaryum is a mainly montane and alpine genus so that it is largely protected from human activity. G. macrocarpum is the species which has been found at the lowest altitudes and probably some of the known populations are near extinction. On the island of Tinos only one small population has survived in dry phrygana in the highest part of the island. Small changes in the vegetation on the islands of Pelagos and Yioura would probably result in the extinction of these populations.

G. bornmuelleri and G. divaricatum have only been collected once. Both the localities cited have been searched carefully by the author but none of the species was found. G. bornmuelleri was collected near Theologos on the island of Thasos and G. divaricatum near Trikala on Mt Killini. The two localities are in areas where human activity is intense and extinction cannot be excluded.

Mainly in the works of L.-A. Gustavsson, B. Aldén, and J. Persson the species of the pumilum-pindicola complex have shown to be common in the high mountains of Greece. G. peloponesiacum, G. pumilum, G. creticum, and G. parnassicum occur on a few mountains only but are common on these mountains.

The three northern species, G. capillifolium, G. tuberosum, and G. cynapioides, are probably commoner than is known today. During the last few years several new finds have been made and in local floras such as Degen (1937) many localities are listed. Further research in the W Turkish mountains will probably show the same situation in G. stylosum.

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CODE TO CULTIVATED MATERIAL

E1. G. macrocarpum. Gr. Naxos. Between Moni and Sifones. 500--700 m.
E2. G. macrocarpum. Gr. Naxos. Between Moni and Sifones. 700 m.
E3. G. macrocarpum. Gr. Naxos. E slope of Fanaris, 1500 m E Moni. 7000 m.
E4. G. macrocarpum. Gr. Tinos. Tzikinia Oros, N slope. 550 m.
E5. G. parnassicum. Gr. Attiki. Mt Parnis, S slope. 1250 m.
E6. G. macrocarpum. Gr. Attiki. Mt Imittos, the top. C. 1000 m.
E7. G. macrocarpum. Gr. Attiki. Mt Imittos, W slope. C. 950 m.
E8. G. macrocarpum. Gr. Rodhos. Mt Prof. Elias. 600 m.
E9. G. euboicum. Gr. Euboea. Mt Dhirfis, E Steni. 750--800 m.
E10. G. macrocarpum. Gr. Pelagos. Just W the monastery, 150 m.
E11. G. capillifolium. Gr. Hagion Oros, 1 km W Kariai. 450 m.
E12. G. peloponesiacum. Gr. Pelop. Mt Panakhaikon, W slope. 1400 m.
E13. G. peloponesiacum. Gr. Pelop. Mt Panakhaikon, W slope. 1650 m.
E14. G. peloponesiacum. Gr. Kefallinia, Mt Ainos. 1400 m.
E15. G. peloponesiacum. Gr. Kefallinia. Mt Ainos. 1450 m.
E16. G. peloponesiacum. Gr. Pelop. Mt Killini, close to the top, 1750 m.
E17. G. peloponesiacum. Gr. Pelop. Mt Killini, close to the top, 2000 m.
E18. G. peloponesiacum. Gr. Pelop. Mt Killini, 8.5 km SSW Trikala, 1750 m.
E19. G. creticum. Gr. Crete. Dhikti Or. 4 km S Ag. Georgios. 1300 m.
E20. G. creticum. Gr. Crete. Dhikti Or. 7 km S Ag. Georgios. 1700 m.
E21. G. pindicola. Gr. Epirus. Mt Peristeri, 10 km S Metsovon. 2050 m.
E22. G. pindicola. Gr. Evrit. Mt Timfristos. Above Karpenision. 2000 m.
E23. G. capillifolium. Gr. Fthiotis. Mt Oiti. 6 km SSE Ipati. 1750 m.
E24. G. pindicola. Gr. Fhiotis. Mt Oiti. 8 km SE Ipati. 1900 m.
E25. G. pindicola. Gr. Fokis. Mt Giona. 4 km S Sthromi. 1500 m.
E26. G. pumilum. Gr. Fthiotis. Mt. Parnassos. 1 km W the top. 2200 m.
E27. G. pumilum. Gr. Fthiotis. Mt Parnassos. W the top. 2100 m.
E28. G. parnassicum. Gr. Achaia. Aroania. 3.5 km SSW Zaroukla. 1700-1800 m. JP.
E29. G. parnassicum. Gr. Arcadia. Mainalon. 2.5 km NW Kardara. 1800 m. JP.
E30. G. parnassicum. Gr. Laconia. Taygetos. 4 km WNW Spartia. 1550 m. JP.
E31. G. parnassicum. Gr. Laconia. Taygetos. 4 km WNW Spartia. 1500 m. JP.
E32. G. parnassicum. Gr. Arcadia. Mainalon. 2 km NW Kardara. 1750-1891 m. JP.
E33. G. parnassicum. Gr. Laconia. Taygetos. Top W Arna. 1590 m. JP.
E44. G. cynapioides. It. Abruzzi. Mt Morrone. 1200 m.
E45. G. capillifolium. It. Gargano. Mt Nero. 650 m.
E46. G. capillifolium. Gr. Khalkidhiki. Mt Ipsiz. 900 m.

E47. G. capillifolium. Gr. Khalkidhike. Mt Ipsiz. 850 m.
E49. G. capill. (tetraploid). Ju. Montenegro. Cakor. 1400 m.
E50. G. capill. (tetraploid). Ju. Montenegro. Cakor. 1800 m.
E51. G. capillifolium. Ju. S. Dalmatia. 5 km SE Kotor. 900 m.
E52. G. tuberosum. Ju. S. Dalmatia. 15 km NNW Kotor. 600 m.
E53. G. tuberosum. Ju. Croatia. Mt Velebit. 900 m.
E54. G. parnassicum. Gr. Arcadia. Parnon. Megala Tourla. 1650 m. JP.
E55. G. peloponesiacum. Gr. Akhaia. Panakhaikon. E Pouranokas. 1800 m. JP.
E56. G. parnassicum. Gr. Laconia. Xeovouna. E Alagonia. 1500-1550 m. JP.
E57. G. peloponesiacum. Gr. Korinthia. Ziria. NW Bousion. 1675-1900 m. JP.
E58. G. parnassicum. Gr. Akhaia. Livadaki. ESE Zarouchla. 1500-1720 m. JP.
E60. G. parnassicum. Gr. Akhaia. Chelmos. SW Zarouchla. 1440-1600 m. JP.
E61. G. parnassicum. Gr. Akhaia. Chelmos. ENE Kato Lousi. 1380-1740 m. JP.
E62. G. peloponesiacum. Gr. Akhaia. Erimanthos. E Kalentsion. 1780-2080 m. JP.
E63. G. parnassicum. Gr. Korinthia. Maurovouni. SW Kastanea. C. 1400 m. JP.
E65. G. macrocarpum. Gr. Rodhos. Ataviros. R. et al.
E66. G. stylosum. Tu. Kemalpasa Dagh. 900 m.
E67. G. stylosum. Gr. Samos. Mt Kerki. C. 1000 m.
E68. G. stylosum Gr. Samos. Mt Kerki. C. 1100 m.
E94. G. macrocarpum. Tu. Antalya. N Cevizli. 1200 m. HR & PW.
E97. G. macrocarpum. Tu. Antalya. N Cevizli. HR & PW.

More material has been in cultivation but for identification and not for experiments presented in this papter.

Collections without initials are collected by the author. JP.: Jimmy Persson, HR.: Hans Runemark, PW.: Per Wendelbo.